THE *CICINDELA SYLVATICA* GROUP: GEOGRAPHICAL VARIATION AND CLASSIFICATION OF THE NEARCTIC TAXA, AND RECONSTRUCTED PHYLOGENY AND GEOGRAPHICAL HISTORY OF THE SPECIES (COLEOPTERA: CICINDELIDAE).[1]

T. G. Spanton
Department of Entomology
The University of Alberta
Edmonton, Alberta T6G 2E3

Quaestiones Entomologicae
24: 51-161 1988

ABSTRACT

The Cicindela sylvatica *species group as defined by Rivalier (1950, 1954) includes the North American species* C. longilabris *Say and* C. nebraskana *Casey, as well as the Palearctic species* C. sylvatica *Linnaeus,* C. granulata *Gebler,* C. japana *Motschulsky,* C. gemmata *Faldermann,* C. soluta *Dejean and* C. lacteola *Pallas.*

Discriminant analysis of morphometric data, univariate analysis of qualitative characters, and study of the distribution and soil associations of adult specimens of Cicindela longilabris *Say and* C. nebraskana *Casey show that* C. longilabris *is a boreal and montane species living on Podzolic soils in eastern North America, and Luvisolic and Brunisolic soils of coniferous forests in western North America, as well as in boreal forest-grassland transition areas. Its three subspecies are: (1),* C. longilabris longilabris *Say, across the boreal zone from Newfoundland and New England to Alaska; (2),* C. l. laurentii *Schaupp, in the Rocky Mountain region of the United States, including isolated populations of northern New Mexico, eastern Arizona, northern Arizona and southwestern Utah; and (3),* C. l. perviridis *Schaupp, living in the Sierra Nevada and Cascade Mountains of California, Oregon and Washington. An area of hybridization includes southwestern Alberta, southeastern British Columbia, eastern Washington, northern Idaho and northwestern Montana where the three subspecies converge geographically.* Cicindela nebraskana *is a monobasic species which lives on Chernozemic soils of prairie grasslands and grassland-forest transition zones of western North America.*

The following new synonymies are presented: Cicindela longilabris longilabris *Say (*=Cicindela longilabris novaterrae *Leng);* C. l. laurentii *Schaupp (*=C. l. oslari *Leng);* C. l. perviridis *Schaupp (*=C. l. ostenta *Casey);* C. nebraskana *Casey (*=C. nebraskana chamberlaini *Knaus).*

[1]Modified from a thesis submitted to Lakehead University, Thunder Bay, Ontario, in partial fulfillment of the requirements for the degree of Master of Science.

Individuals of C. longilabris *live for three years: two winters are passed in the larval stage and one winter in the adult stage before mating and oviposition.*

A male neotype specimen is designated for the species C. longilabris *Say, from Ontario, Thunder Bay District, Sibley Provincial Park, 1 km W of Silver Islet.*

Phylogenetic analysis shows three pairs of sibling species: C. soluta-C. gemmata, C. sylvatica-C. granulata *and* C. longilabris-C. nebraskana, *with* C. japana *most closely related to the* soluta-gemmata *pair.* Cicindela lacteola *was either derived earlier in the evolution of the group; or in the absence of a synapotypy for* C. lacteola *and the other species of the group, it is possible that this species should not be classified in this species group.*

RÉSUMÉ

Le groupe-espèce Cicindela sylvatica *definis par Rivalier (1950, 1954) inclus l'espèces Nord Américaines* Cicindela longilabris *Say, et* Cicindela nebraskana *Casey, de même que les espèces paléartiques* C. sylvatica *Linnaeus,* C. granulata *Gebler,* C. japana *Motschulsky,* C. gemmata *Faldermann,* C. soluta *Dejean et* C. lacteola *Pallas.*

L'analyse discriminante des données morphométriques, l'analyse univariée des charactères qualitatifs, ainsi que l'association entre le type de sol et les adultes de Cicindela longilabris *Say et de* C. nebraskana *Casey démontrent que* C. longilabris *est une espèce boréale et de montagne habitant sur les sols Podzoliques de l'est de l'Amérique du Nord, et sur les sols Luvisoliques et Brunisoliques des forêts de conifères de l'ouest du continent, ainsi que dans les régions de transition entre prairie et forêt boréale. Ses trois sous-espèces sont: (1),* C. longilabris longilabris *Say (zone Boréale entre Terre-Neuve, la Nouvelle Angleterre et l'Alaska); (2),* C. l. laurentii *Schaupp, (régions des Montagnes Rocheuses des étas-Unis, incluant des populations isolées du nord du Nouveau Méxique, de l'est et du nord de l'Arizona, et du sud-ouest de l'Utah); et (3)* C. l. perviridis *Schaupp, (Sierra Nevada et les montagnes Cascades de la Californie, Oregon et Washington). Une région d'hybridation inclus le sud-ouest de l'Alberta, le sud-est de la Colombie Britannique, l'est de l'état de Washington, le nord de l'Idaho et le nord-ouest du Montana, où les trois sous-espèces convergent géographiquement.* Cicindela nebraskana *est une espèce monotypique qui habite les sols Chernozemiques des prairies et des régions de transition prairie - forêt boréale de l'ouest de l'Amerique du Nord.*

Les nouvelles synonymies suivantes sont présentées: Cicindela longilabris longilabris *Say (*=C. l. novaterrae *Leng);* C. l. laurentii *Schaupp (*=C. l. oslari *Leng);* C. l. perviridis *Schaupp (*=C. l. ostenta *Casey);* C. nebraskana *Casey (*=C. n. chamberlaini *Knaus).*

Les individus de C. longilabris *ont une longévité de trois ans: ils vivent deux hivers au stade larvaire, et le troisième au stade adulte avant d'engager la copulation et l'oviposition le printemps suivant.*

Un specimen néotype, mâle est désigné pour l'espèce C. longilabris *de l'Ontario, district de Thunder Bay, Parc Provincial de Sibley, 1 km ouest de Silver Islet.*

L'analyse phylogénique démontre qu'il y a trois paires d'espèces-soeurs: C. longilabris-C. nebraskana, C. sylvatica-C. granulata, *et* C. soluta-C. gemmata, *avec* C. japana *s'apparentant le plus à la paire* C. soluta-C. gemmata. Cicindela lacteola *c'est développée, soit très tôt au cours de l'évolution du groupe, soit en l'absence d'une synapotypie entre* C. lacteola *et les autres espèces du groupe, il est possible que cette espèce ne devrait pas être classifiée dans ce groupe-espèce.*

TABLE OF CONTENTS

INTRODUCTION

The adults of most taxa of tiger beetles in the Nearctic and Palearctic regions have been described and named for some time, but only in the past 20 years have extensive studies of intraspecific variation, and classification of species groups of *Cicindela* been conducted. For example, Freitag (1965) studied the geographic variation and distribution and revised the North American species of the *Cicindela maritima* group. Willis (1967) studied geographic variation and ecology of a diverse group of *Cicindela* species living in saline habitats in the central United States, Gaumer (1977) studied intraspecific variation and taxonomy of adults and larvae of *C. formosa*, Murray (1980) studied geographic variation of *C. rufiventris* Dejean, *C. sedecimpunctata* Klug, and *C. flohri* Bates, and Kaulbars (1982) studied the morphological and ecological variation of the species of the *C. sexguttata* species group.

Wallis (1961) confused many of the intraspecific taxa of *C. longilabris* and *C. nebraskana* but indicated that his understanding of these species was based on few specimens and suggested that this group required additional study. Leffler and Pearson (1976) indicated that revisionary study of *C. nebraskana* and *C. longilabris* was required to establish the taxa and to correctly apply the available names.

The immature stages and life histories of a number of tiger beetle species have been studied (Shelford, 1908; Criddle, 1907, 1910; Hamilton, 1925; Willis, 1967, among others) but the life histories of *C. longilabris* and *C. nebraskana* are largely unknown. The larvae of *C. longilabris* are known only from one third instar specimen and three exuviae (Leffler, 1979).

This study began as an investigation of the patterns of geographic variation in the *Cicindela longilabris-C. nebraskana* complex. For this reason a detailed treatment of the Nearctic taxa of the *C. sylvatica* group is presented. After investigating genitalic structures of the members of the *C. longilabris-C. nebraskana* complex, similar genitalic dissections were made of the other species in the *sylvatica* group to determine what degree of structural difference might occur among the species of the group. As some synapotypies became apparent in genitalic structures, I decided to carry out a cladistic analysis to hypothesize phylogenetic relationships among the species of the group. Detailed study of the pattern of geographical variation of the Palearctic species was beyond the scope of this study.

The objectives of this study were: (1), to determine if *C. longilabris* and *C. nebraskana* are conspecific, or distinct species; (2), to investigate the pattern of intraspecific variation in these species; (3), to establish the North American taxa and correctly apply the available names; (4), to investigate the life history of *C. longilabris* and describe immature life stages, as possible; and (5), to carry out a phylogenetic analysis of the species of the *C. sylvatica* group to hypothesize relationships among the taxa.

MATERIALS AND METHODS

Material: Adult Specimens and Loaning Institutions

More than 6,210 adult specimens were examined. Most specimens were obtained on loan from the following institutions and private collections. I have used standard codens for collections of insects as proposed by Heppner and Lamas (1982), wherever possible. For private collectors, initials were used as codens. Curators, and/or staff members with whom I corresponded, are named following their respective institutional addresses.

AAM	Alan and Anne Morgan, Departments of Earth Sciences and Biology respectively, University of Waterloo, Waterloo, Ontario N2L 3G1
AMNH	American Museum of Natural History, New York, New York 10024; L. H. Herman
BGSU	Bowling Green State University, Bowling Green, Ohio 43403; R. C. Graves
CAS	California Academy of Sciences, San Francisco, California 94118; D. H. Kavanaugh
CDF	Clifford D. Ferris, P. O. Box 3351, University Station, Laramie, Wyoming 82071
CMP	Carnegie Museum of Natural History, Pittsburgh, Pa. 15213 ; R. L. Davidson
CNC	Canadian National Collection of Insects, Biosystematics Research Centre, Ottawa, Ontario K1A 0C6; J. E. H. Martin
CSU	Colorado State University, Fort Collins, Colorado 80523; H. E. Evans

CU	Cornell University, Ithaca, New York 14853; L. L. Pechuman, Q. D. Wheeler
ISU	Iowa State University, Ames, Iowa 50011; R. E. Lewis
KSU	Kansas State University, Manhattan, Kansas 66506; H. D. Blocker
MPM	Milwaukee Public Museum, Milwaukee, Wisconsin 53233; G. R. Noonan
MSU	Montana State University, Boseman, Montana 59717; S. Rose
MUN	Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9; D. J. Larson
NAU	Northern Arizona University, Flagstaff, Arizona 86001; C. D. Johnson
NCSR	North Carolina State University, Raleigh, NC 27650; C. Parron
NDSU	North Dakota State University, Fargo, ND 58105; E. U. Balsbaugh
OKS	Oklahoma State University Natural and Cultural History Museum, Stillwater, OK; W. A. Drew
PSU	Pennsylvania State University, University Park, PA 16802; D. L. Pearson
PUL	Purdue University, Lafayette, Indiana 47907; A. Provonsha
REA	Robert E. Acciavatti, 2111 Cherry Street, Morgantown, West Virginia 26505
SMEK	Snow Museum of Entomology, University of Kansas, Lawrence, KS 66045; G. W. Byers
UAE	University of Alberta, Edmonton, Alberta T6G 2E3; G. E. Ball, D. Shpeley
UAF	University of Arkansas, Fayetteville, Arkansas 72701; R. Chenowith, C. Carleton
UBC	University of British Columbia, Vancouver, B.C.; S. G. Cannings
UIM	University of Idaho, Moscow, Idaho 83843; W. F. Barr
UMAA	University of Michigan, Ann Arbor, Michigan 48109; T. E. Moore, M. F. O'Brien
UMW	University of Manitoba, Winnipeg, Manitoba R3T 2N2; T. D. Galloway
UNM	University of New Mexico, Albuquerque, NM 87131; C. S. Crawford
UOG	University of Guelph, Guelph, Ontario N1G 2W1; D. Pengelly, S. A. Marshall
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; T. L. Erwin
USU	Utah State University, Logan, Utah 84322; W. J. Hanson
UV	University of Vermont, Burlington, Vermont; R. T. Bell
UWM	University of Wisconsin, Madison, Wisconsin 53706; S. Krauth
WJ	Walter Johnson, 2917 16th Avenue South, Minneapolis MN 55407
WSU	Washington State University, Pullman. WA 99164; R. Zack

Additional specimens were acquired by field collecting. During a ten week collecting trip in the summer of 1981, specimens were collected *in situ* and observations were made of the habitats of these beetles over much of the geographic

range of *C. longilabris* and *C. nebraskana* in Canada and the United States. Specimens were also collected in the summer of 1982 in western Ontario and northern Minnesota.

Methods

Characters and measurements.— A number of measurements were taken to investigate differences in size and body proportions among populations of species of the *C. longilabris-C. nebraskana* complex.

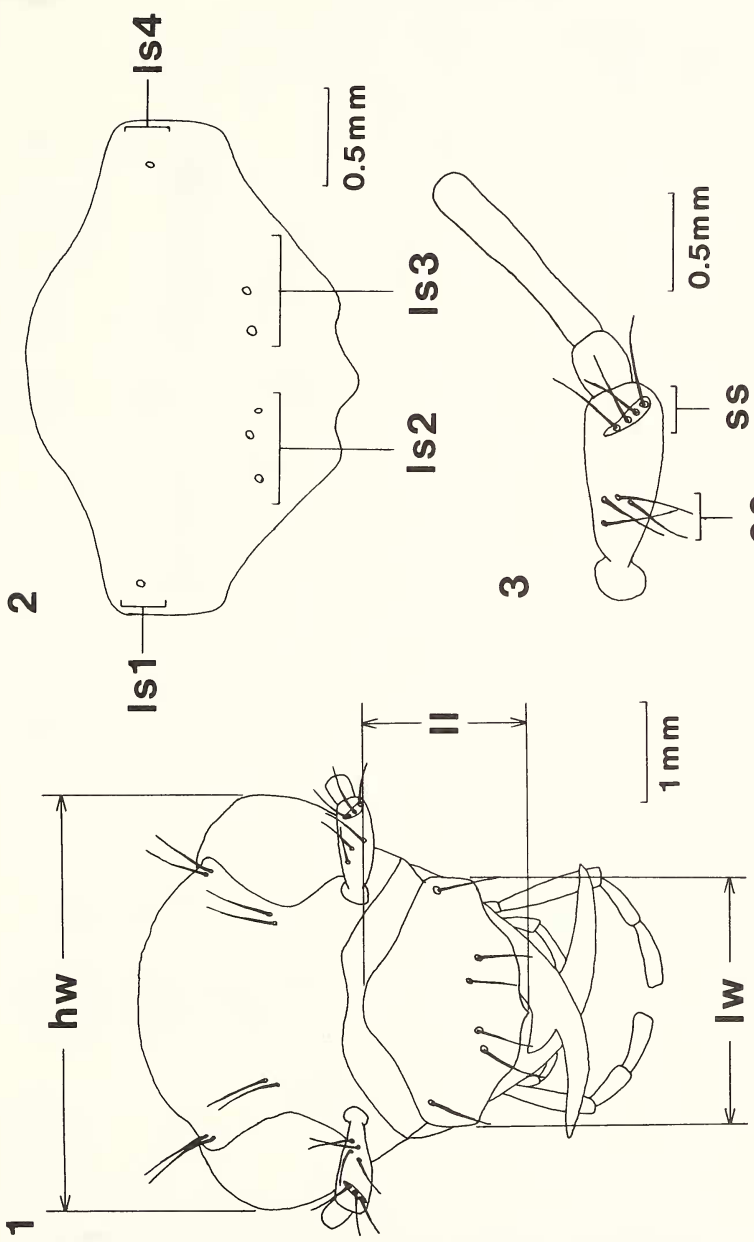
Characters of the labrum of the adult stage were examined because the large size of the labrum in *C. longilabris* and *C. nebraskana* has been used to distinguish between these and other North American tiger beetle species (Willis, 1968), and because the color of the labrum is dark in many specimens of *C. nebraskana*, especially in females, whereas it is light tan in most specimens of *C. longilabris* (Leffler, 1979).

The number and pattern of setae on the antennal scape has been used to distinguish among species of *Cicindela* (Willis, 1968).

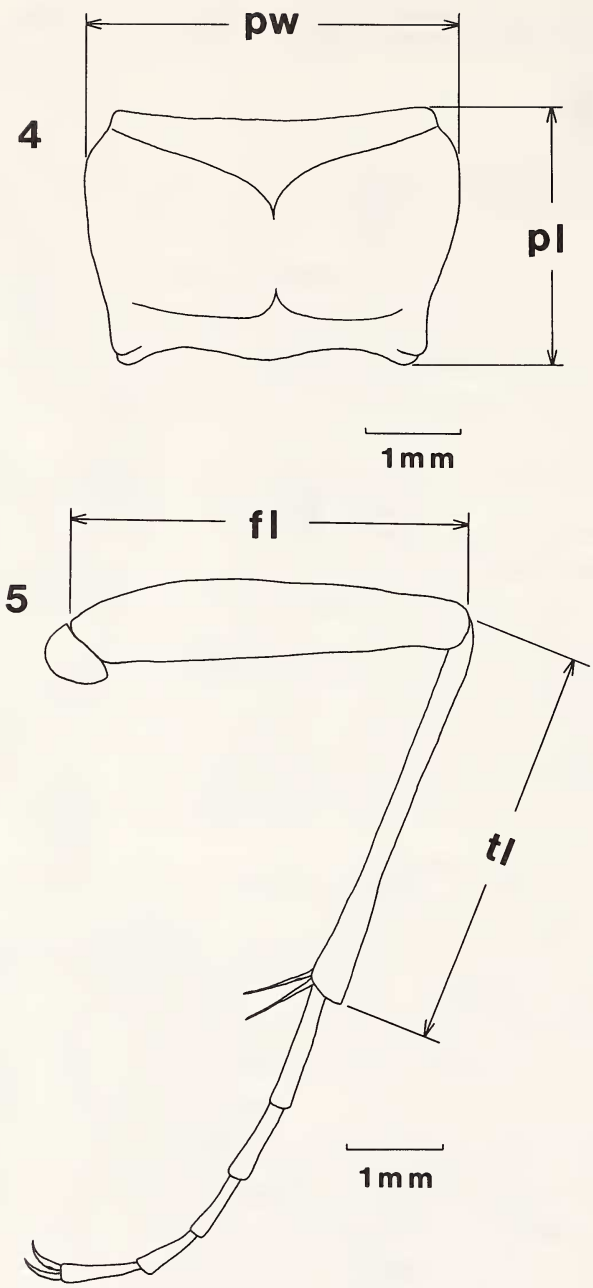
Color and pattern of markings have figured prominently in descriptions of tiger beetles. In many groups of tiger beetles, and especially in the *C. longilabris-C. nebraskana* complex, many specific and subspecific names have been applied to individual variants, and to variant populations, based solely on differences in color and pattern of markings. I attempted to elucidate the pattern of variation in characters of color and color pattern, across the range of these two species. The following characters were used in either the numerical analyses, or qualitative character analyses of this study. The alphanumeric characters in brackets following each character listed below are abbreviations used in this paper.

1. Total head width across the widest point on the eyes (hw)(Fig. 1)
2. Length of labrum including the median tooth (ll)(Fig. 1)
3. Width of labrum (lw)(Fig. 1)
4. Ratio: length of labrum/width of labrum (ll/lw)
5. Color of labrum (lcol). I arbitrarily assigned three states for this character.
    1. uniformly pale in color, or pale except for a darkened apical margin.
    2. apical margin and midrib broadly darkened or mottled.
    3. uniformly dark brown or black.

    The setal pattern on the labrum was used as a set of characters (6–9).The number of setae in each of four locations on the frontal surface of the labrum was indicated (Fig. 2). Each of these loci was treated separately because the number of setae was, in many instances seen to vary from one side of the animal to the other (i.e. positions 1 and 4; positions 2 and 3).
6. Number of setae in position 1 (ls1)
7. Number of setae in position 2 (ls2)
8. Number of setae in position 3 (ls3)



Figs. 1–3. Characters of the adult head. 1. Head, frontal aspect: hw, head width; ll, labrum length; lw, labrum width. 2. Labrum, frontal aspect: ls1, setae at position one; ls2, setae at postion two; ls3, setae at position three; ls4, setae at position four. 3. Left antenna, frontal aspect: the scape; ss, sensory setae; os, other setae.



Figs. 4–5. 4. Adult prothorax, dorsal aspect: pw, pronotal width; pl, pronotal length. 5. Left mesothoracic leg, anterior aspect: fl, femur length; tl, tibial length.

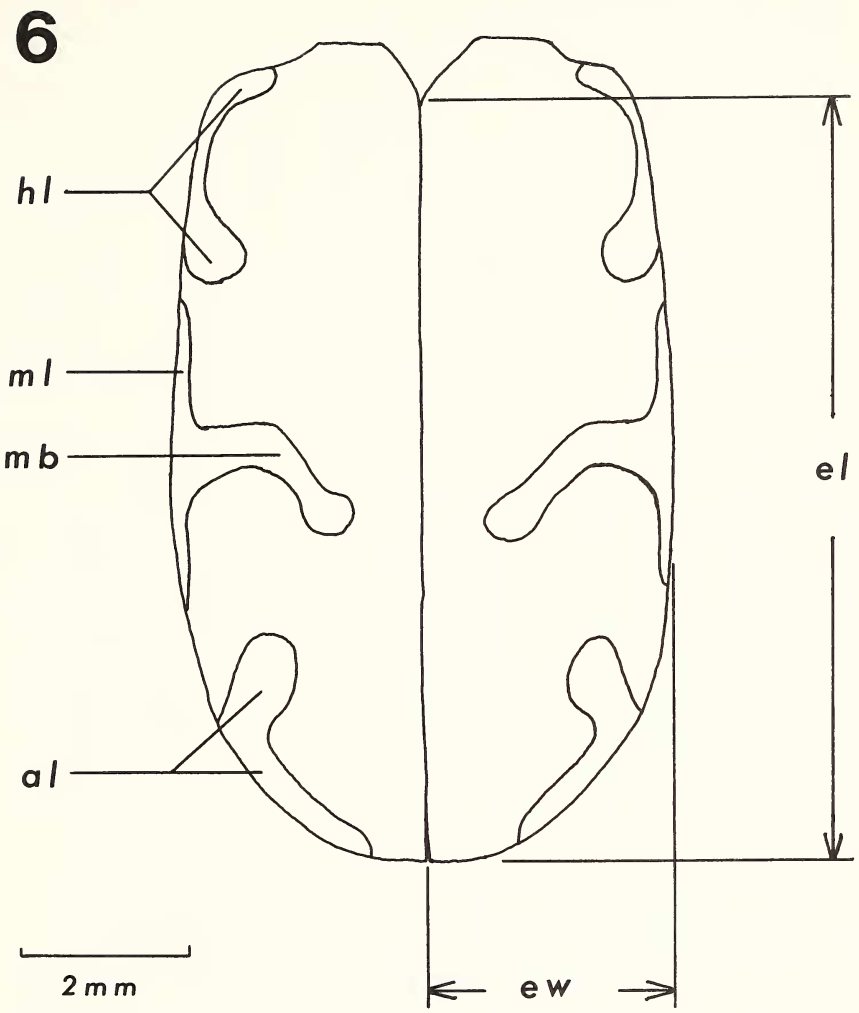


Fig. 6. Adult elytra, dorsal aspect: el, elytral length; ew, elytral width; hl, humeral lunule; mb, middle band; ml, marginal line; al, apical lunule.

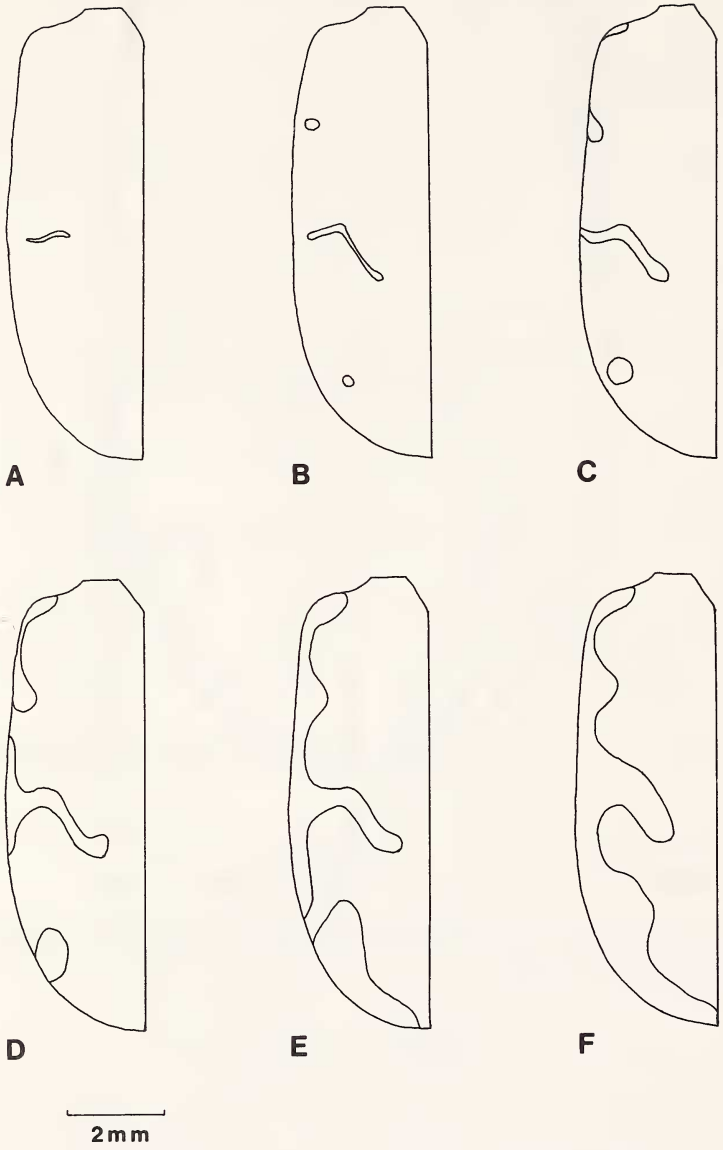


Fig. 7. Percent of elytral surface covered by maculations: A, one per cent; B, two per cent; C, five per cent; D, ten per cent; E, twenty per cent; F, thirty per cent.

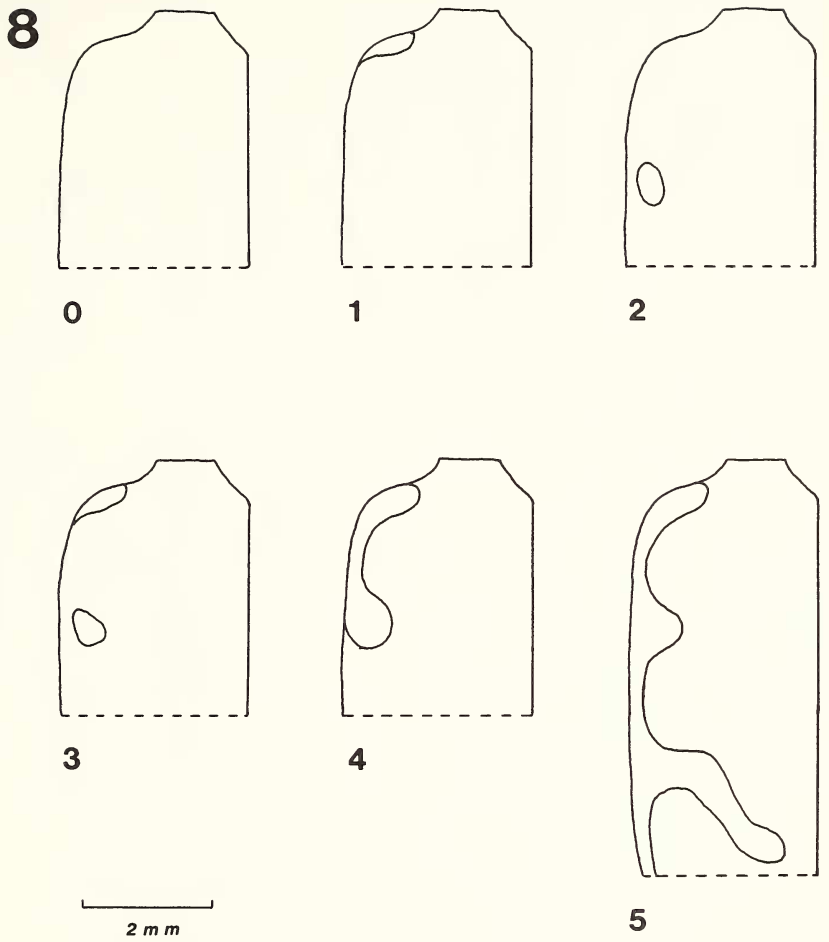


Fig. 8. Humeral lunule character states. The number at the lower left of each drawing indicates arbitrarily assigned values.

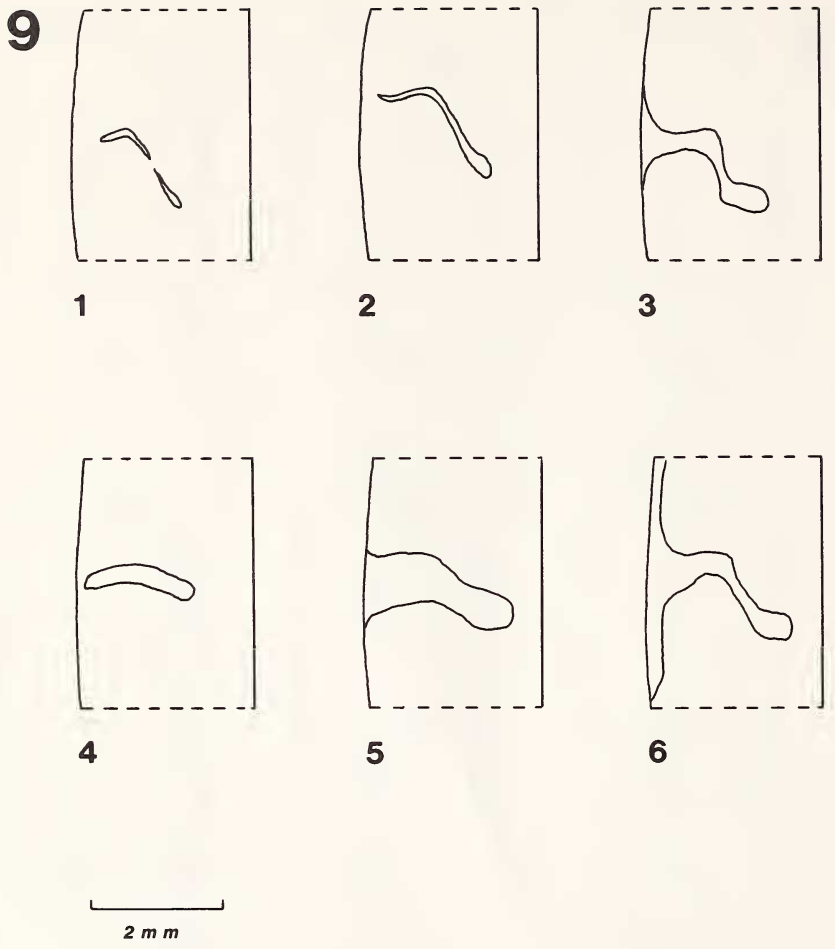


Fig. 9. Middle band character states. The number at the lower left of each drawing indicates arbitrarily assigned values. A zero was assigned if the middle band was absent.

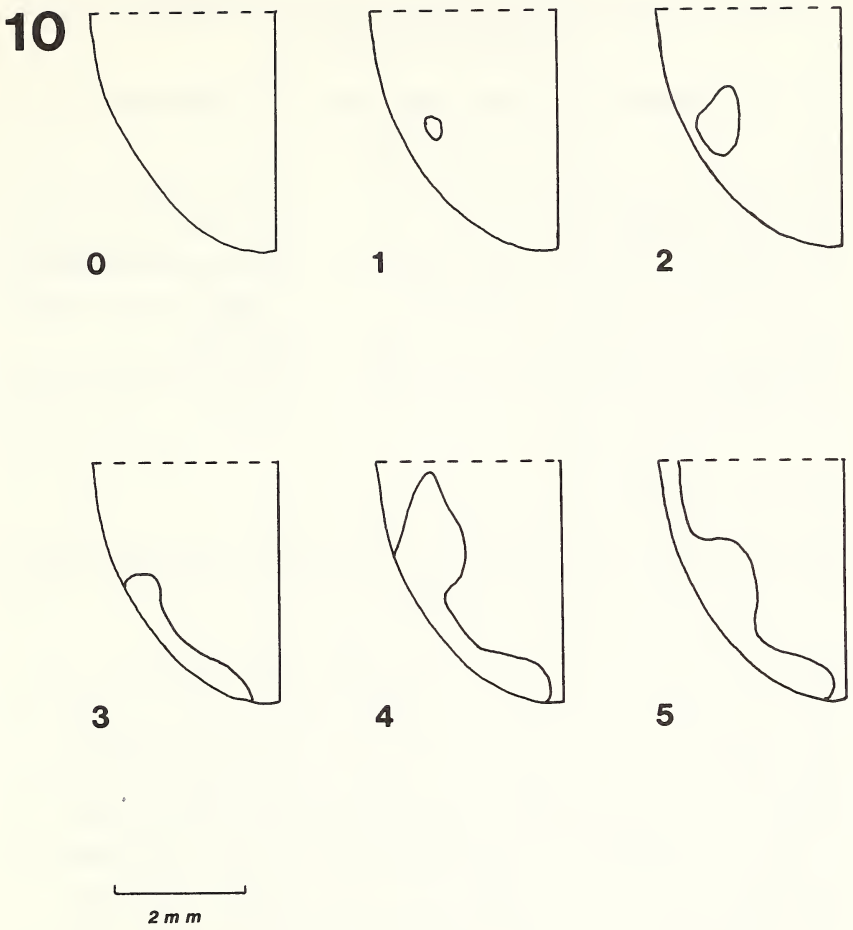


Fig. 10. Apical lunule character states. The number at the lower left of each drawing indicates an arbitrarily assigned value.

TABLE 1. Designated states for color of the dorsal surface of elytra of *C. longilabris* and *C. nebraskana*.

Vernacular description	Code	ISCC-NBS Number*	ISCC-NBS Name
Black	1	267	Black
Dark Brown	2	65	Brownish Black
Mid Brown to Bronze	3	56	Deep Brown
Olive Green	4	108 or 111	Dark Olive or Dark Grayish Olive
Green	5	142	Deep Green
Blue Green	6	174	Dark Greenish Blue
Dark Blue	7	183	Dark Blue

*Kelly and Judd, 1965.

TABLE 2. Designated states for color of the proepisternum of *C. longilabris* and *C. nebraskana*.

Vernacular description	Code	ISCC-NBS Number*	ISCC-NBS Name
Shining Black	1	267	Black
Black and Green	2	267 and 142	Black and Deep Green
Metallic Green	3	142	Deep Green
Metallic Green and Blue, or Metallic Green and and Purple	4	142 and 183 or 142 and 197	Deep Green and Deep Blue, or Deep Green and Deep Purplish Blue
Blue and/or Purple Predominantly	5	183 and/or 197	Deep Blue and/or Deep Purplish Blue
Bronze and Metallic Green or Bronze and Purple in combination	6	75 and 142 or 75 and 197	Deep Yellowish Brown and Deep Green or Deep Yellowish Brown and Deep Purplish Blue
Bronze to Chestnut Brown predominantly	7	75 and 56	Deep Yellowish Brown to Deep Brown

*Kelly and Judd, 1965.

TABLE 3. Designated states for color of the venter of the abdomen of *C. longilabris* and *C. nebraskana*.

Vernacular description	Code	ISCC-NBS Number*	ISCC-NBS Name
Black	1	267	Black
Black and Green	2	267 and 142	Black and Deep Green
Metallic Green	3	142	Deep Green
Metallic Green and Blue, or Metallic Green and Purple	4	142 and 183, or 142 and 197	Deep Green and Deep Blue, or Deep Green and Deep Purplish Blue
Blue and/or Purple predominantly	5	56 and 142, or 56 and 197	Deep Brown and Deep Green, or Deep Brown and Deep Purplish Blue
Brown predominantly	7	56	Deep Brown

*Kelly and Judd, 1965.

9. Number of setae in position 4 (ls4)
10 Number of sensory setae on the first antennomere (scape) of the left antenna (ssl) (Fig. 3)
11 Number of sensory setae on the scape of the right antenna (ssr)
12 Number of other setae on the scape of the left antenna (osl)
13 Number of other setae on the scape of the right antenna (osr)
In characters 10 to 13 the corresponding number of setae on left and right sides were treated separately because this was seen to vary in some instances from left to right antenna of the same individual.
14 Pronotal width (pw)(Fig. 4)
15 Pronotal length (pl)(Fig. 4)
16 Ratio:pronotal width/pronotal length (pw/pl)
17 Mesothoracic femur length (fl)(Fig. 5) The left mesothoracic leg was chosen preferentially. Where the left was missing, the same measurement was taken from the right leg. The mesothoracic leg was chosen because prothoracic and metathoracic legs were more frequently missing from pinned specimens.
18 Mesothoracic tibia length (tl)(Fig. 5)
19 Ratio: mesofemur length/mesotibia length (fl/tl)
20 Length of left elytron (el)(Fig. 6). This was measured from the apex of the scutellum along the suture to its apex.
21 Width of left elytron at its widest point (ew)(Fig. 6). This was measured with

the beetle held in a horizontal plane.

22 Ratio: head width/pronotal width (hw/pw)

23 Ratio: elytral width/elytral length (ew/el)

24 Ratio: femur length/elytral length (fl/el)

25 Per cent of elytral surface covered by light markings or maculations. This was estimated in a manner very similar to that used by Gaumer (1977). A series of specimens representing the range of variation present in *C. longilabris* and *C. nebraskana* was selected. A drawing was made of the left elytron of each specimen. A polar planimeter was used to determine the percentage of each elytron covered by the maculations. Subsequently, these drawings were used as standards of comparison for estimating the percentage to the nearest one of six categories: 1%, 2%, 5%, 10%, 20%, and 30% (Fig. 7).

26 The configuration of the humeral lunule (hl). I recognized the following six states of this character (Fig. 8):

0. humeral lunule absent.
1. one humeral dot present at shoulder of elytron.
2. one subhumeral dot present.
3. both humeral dots present.
4. humeral lunule complete, or nearly so.
5. humeral lunule complete and connected to marginal line.

27 The configuration of the middle band (mb). Specimens were categorized as being closest to one of the following states of this character (Fig. 9):

0. middle band completely absent.
1. middle band barely discernible, or in two pieces.
2. middle band present, with angle of bend greater than 45 degrees, and not touching lateral margin of elytron.
3. band complete, touching lateral margin of elytron and angle of bend greater than 45 degrees.
4. band present, not touching lateral margin of elytron and elbow less than 45 degrees.
5. middle band complete, touching lateral margin and elbow less than 45 degrees.
6. band complete, touching lateral margin, and marginal line well developed.

28 Apical lunule character states (al) The following states were recognized in the degree of development of the apical lunule (Fig. 10):

0. apical lunule entirely absent.
1. apical lunule consists of a small subapical dot.
2. apical lunule consists of a large subapical dot.
3. apical lunule complete.
4. lunule complete, with dot expanded anteriorly.
5. apical lunule complete and continuous with marginal line

anteriorly.

30 Color of dorsal surface of elytra (ec)(Table 1)

31 Color of proepisternum (pc)(Table 2)

32 Color of ventral surface of abdomen (vc)(Table 3)

Tables 1–3 contain a vernacular designation of a color condition, the character state number and corresponding name and number from the ISCC-National Bureau of Standards Color Charts (Kelly and Judd, 1965). For each of characters 29, 30, and 31 a small series of specimens was chosen to represent the range of variation found in the *C. longilabris* species complex. These standard specimens were compared with the ISCC-National Bureau of Standards Color Charts and the corresponding color name and number were noted. If a specimen did not closely match any one color, the two or three colors closest to it were noted. Subsequently, each studied specimen was compared against standard specimens and designated as being closest to one of the representative color categories.

One difficulty with this method is that many of the colors of tiger beetles are structural (Shelford, 1917) and have a metallic sheen, whereas those of the standard color charts are opaque. The color of the dorsal surface of elytra was designated a single color state. For color of the proepisternum and venter of the abdomen, each character state was, in many specimens, a mosaic of more than one color, which added to the problem.

Measurements and character states were taken from adult specimens from 60 localities across the range of the species complex: 12 population samples of *C. nebraskana* and 48 of *C. longilabris* (Fig. 11, Table 4). An effort was made to choose larger population samples. While only small samples were available from many localities, they were analyzed with the knowledge that they may have been atypical because of biased sampling by collectors. Collectors may take disproportionately large numbers of unusual color morphs in preference to common morphs, especially of the common species.

Numerical analysis of morphometric data.— Sexual dimorphism was examined by comparing males and females for each of the variables using a one-way analysis of variance (ANOVA) procedure as described by Kim and Kohout (1975). With the probability of a type one error set at 0.05, significant sexual dimorphism was found in both *C. nebraskana* and *C. longilabris* . Females of both groups showed significantly larger measurements in head width, labrum width, labrum length, pronotal width and length, and elytral width and length, suggesting that females of both species are significantly larger in overall size. In all subsequent analyses of morphometric data males and females were treated separately. All analyses were performed with the use of a Vax 11/780 computer.

Discriminant analyses based on the above series of measurements were performed to investigate differences among population samples. The discriminant procedure used was described by Klecka (1975) and was taken from the Statistical

Package for the Social Sciences for Vax.VMS, Version M, Release 8.1, May 1, 1981.

A linear discriminant function is a combination of character scores which discriminates between groups much better than one character taken singly (Sneath and Sokal, 1973). For this reason significance levels of 0.05 or 0.01 are not useful in this type of analysis, since they identify taxonomically insignificant differences. Some neighbouring populations which appeared to be very similar were significantly different beyond the 0.01 level in these analyses. A significance level of 0.001 was selected as the minimum requirement indicative of a taxon. However, no taxonomic decisions were based entirely on the evidence of discriminant analysis.

For seemingly important population groupings established by discriminant analyses, additional one-way analyses of variance were used (Kim and Kohout, 1975) to investigate the statistical differences in those variables which scored highest in the discriminant functions.

Analysis of color and pattern of markings.— Color variation was demonstrated with the use of pie graphs on distribution maps (Figs. 12–19) in a manner similar to that used by Freitag (1965), Willis (1967), and Gaumer (1977). Mean states of additional characters for each population sample are summarized in Table 11 and are indicated with symbols on maps in a way similar to that used by Goulet and Baum (1981, 1982).

Dissections of male and female genitalia.— Using standard methods, genitalia of male and female specimens of many populations of *C. nebraskana* and *C. longilabris* were examined for structures of taxonomic importance. Males and females of six Palearctic species (not more than two or three specimens of each gender, per species) were dissected to aid in determining relationships among the species of the *C. sylvatica* group. In all 170 genitalic dissections were performed.

Soil associations.— Collecting localities from specimen label data were located on national scale and state soil maps to seek relationships between the distribution of dominant soil types and the distribution of the different forms of the *C. sylvatica* group in North America. Conversions between the United States and Canadian systems of soil classification were made with tables provided in Clayton *et al.* (1977). Descriptions of soil types were followed in Clayton *et al.* (1977) for the Canadian classification and in Soil Survey Staff (1960, 1967) for the American system.

Dates of collection were used to plot histograms of frequency of capture versus date to investigate seasonality in adults of *C. longilabris* and *C. nebraskana*, and other label data were used to compile distribution lists and to plot distribution maps of the two North American species.

Field methods.— Adult specimens were collected with an insect net, killed in an ethyl acetate jar and either pinned the same day or transferred to 70% ethanol for temporary storage. Larvae were collected in one of two ways. The "lie in wait"

method involved waiting near the mouth of an open burrow until the larva appeared near the surface, at which time a small shovel was driven at an angle under the larva, cutting off its escape route. The other method was to dig out the larva with a hand trowel. As larvae of *C. longilabris* were found at depths to 60 cm, it was helpful to insert a long piece of flexible grass into the burrow until the larva was felt at the bottom. A hole was then dug beside the stalk of grass until the larva was encountered. Larvae were either preserved directly in 70% ethanol or were placed live in a glass vial with a small amount of soil for transport to the laboratory.

Samples of soil were collected from larval sites and transported to the laboratory where they were thoroughly dried in an oven and if necessary, rolled gently with a rolling pin to break up any aggregations which formed during drying. Each sample was then shaken through a standard sieve series with mesh sizes of 2.0 mm, 0.50 mm, 0.25 mm, 0.125 mm, 0.063 mm and 0.037 mm to determine the distribution of soil particle sizes.

Study sites.— One site, located in the Thunder Bay district of Ontario near the east bay of Dog Lake, 1–5 km W of highway 527 and 50 km N of highway 17, was used primarily as a source of specimens, both for mating experiments and for rearing larvae. The species *C. longilabris* was found along logging roads that extend through second growth forest in an area of sandy soil where the dominant trees were Trembling Aspen (*Populus tremuloides* Michx.) and Jack Pine (*Pinus banksiana* Lamb.) and through an area of slightly more gravelly soil with Trembling Aspen, Jack Pine and Spruce (*Picea* sp.). Ground cover varied from absent on the road surface to patchily distributed mosses and lichens, grasses, wild strawberry (*Fragaria virginiana* Duch.) and leaf litter.

The other study site, at Stanley Hill Cemetery on highway 17, 16 km W of Thunder Bay, Ontario, included some of the grounds of the cemetery, a small sandy area along the edge of forested land across the highway from the cemetery, and part of a pasture bordering the cemetery on the east side. This was an area of sandy soil with vegetation cover ranging from mixed forest of predominantly Trembling Aspen and Jack Pine to old field habitat and bare soil.

A bare road surface extended along the edge of the field. The south end was in close proximity to Jack Pine trees, and the north end extended into an open field habitat. This road was marked at intervals of approximately 5 meters for a distance of 800 meters.

A multiple mark and recapture study was conducted at this site through the summer of 1982 to investigate mobility and relative abundance of the adult beetles. Beetles were captured with a net. Marks were placed on the elytra in the form of small dots of enamel model paint, which has been used successfully in mark and recapture studies of tiger beetles (Willis, 1974; Palmer, 1976; Kaulbars, 1982), and numerous other insects (Southwood, 1978). Using six locations on each elytron where spots could be placed, and six colors of paint, 468 different combinations of marks were possible with no individual bearing more than two spots. Each captured

beetle was marked and released at the point of capture and its sex, location and date of capture were recorded. Each capture session consisted of one survey from one end of the 800 meters of marked road surface to the other, and back again. On days when few beetles were captured this took approximately two hours; when beetles were numerous a capture session was limited to three hours. Capture/recapture sessions throughout the summer were conducted mainly on sunny, warm days.

The chronology of larval development was studied at the Stanley Hill site by marking burrows. A golf tee numbered with a waterproof ink marker was placed 2 cm north of each burrow, and the developmental stage inferrred from the size of the head and pronotum and the diameter of the burrow. Both the size of head and pronotum and the diameter of the burrow show three discrete size categories corresponding to the three larval instars. Burrows were checked at intervals of a few days to a week throughout the summer. Newly found burrows were marked and each burrow was noted as open or closed, and if open the instar was recorded.

In the middle to latter half of the summer, 1st instar larval burrows appeared in numbers too large for all to be marked with golf tees. At this time visual counts were made of open burrows in each stage of development at intervals of a few days to a week to gather information on the seasonality of the larval stages.

Rearing techniques.— Live adults were kept in glass terraria approximately 15 cm x 40 cm x 25 cm in size, the bottom of which were covered to a depth of approximately three cm at one end to six cm at the other end with soil taken from the site where the beetles were captured. A petri dish filled to the level of the rim with soil was placed in the shallow end of each terrarium and periodically filled to overflowing with water. In this way soil moisture available to the beetles ranged from wet in and around the petri dish at one end of their enclosure to dry at the other end. Two to three adults of both sexes were placed in each terrarium. Initially, mortality from cannibalism was high until clumps of mosses, grasses and leaf litter from the beetles' natural habitat were added to the terraria. The tiger beetles immediately used the leaf litter for cover or dug shallow burrows under the clumps of grass or moss. Aggressive encounters and cannibalism were greatly reduced after these modifications. The beetles were fed primarily flour beetles (*Tribolium* spp.) supplemented occasionally with assorted arthropods collected with a sweep net.

First instar larvae which appeared in the terraria subsequent to mating and oviposition, and other larvae dug from the field were reared in glass tubes approximately 2 cm in diameter by 30 cm long in a manner similar to that described by Palmer (1979). The rearing tubes were plugged at the bottom with wet cotton balls or crumpled paper towelling and filled to a depth of 20 - 25 cm with soil from the site where the larvae were collected, or for those produced in the laboratory, where their parents were collected. The rearing tubes were placed on end in a plastic bucket and the soil kept slightly moist with water added to the bucket and occasionally applied to the surface with a plant sprayer. Soil moisture was regulated to minimize mould growth. In a few instances mould developed and specimens were

lost. First instar larvae of *Cicindela* were fed early instar larvae of *Tribolium* spp. and second and third instar tiger beetle larvae were fed late instar larvae, pupae and adult *Tribolium* .

In the laboratory the ambient temperature was approximately 20°C, with fluorescent lights which were generally on during the day and off at night. No attempt was made to approximate naturally occurring photoperiod, temperature, or humidity. Palmer (1979) noted that fecundity of some species of tiger beetles is reduced under laboratory conditions and suggested that temperature may be important in egg production. Reproductive success may have been increased if laboratory conditions more closely approximated the warm daytime temperatures, cool nights and long photoperiod typical of summer in their natural environment.

Criteria for species and subspecies.— Species concepts have been discussed by Simpson (1961), Mayr (1969) and Wiley (1981), among many others. The use of a subspecific category has in the past been controversial among zoologists, with workers such as Edwards (1954), Parkes (1955), and Smith and White (1965) arguing in favour of its use, and Wilson and Brown (1953), Gosline (1954), Hubble (1954) and Owen (1963), among others, opposed to its use. More recently, it seems that many ornithologists (Mayr, 1982; Parkes, 1982; Gill, 1982; Storer, 1982; Barrowclough, 1982; Lanyon, 1982; Johnson, 1982; Zusi, 1982; Monroe, 1982; O'Neill, 1982; Phillips, 1982) feel that the subspecific category should be retained in zoological nomenclature and that trinomina are at least of practical value in some instances. Virtually all of these more recent essays express some reservations regarding the use of subspecific names. Taken to extremes, the formal naming of minutely different populations has little meaning biologically, and merely confuses the nomenclature. This has certainly been a problem in tiger beetle taxonomy when in the past, many subspecies and species names have been formally proposed, based on one or very few variant specimens. Other concerns regarding subspecies include, (1), the tendency for different characters to show discordant patterns of geographic variation; (2), the occurrence of similar or phenotypically indistinguishable populations in geographically separated areas (the "polytopic subspecies" of Mayr, 1969); (3), that an artificial compartmentalization of our concept of the pattern of variation in a species tends to obscure geographic variation within subspecies; (4), the subjectivity in the degree of distinction required by different workers to justify the application of a formal name.

Advantages of the use of a subspecies category are many. Subspecies names are important sorting devices for curators of collections, even if this is strictly a clerical convenience. Trinomina are useful in information retrieval, as much information regarding genetics, population dynamics, feeding behavior, and other aspects of an organism's biology have been published on certain subspecies of polytypic species. Ironically, as Mayr (1982) points out, searching of collections for possible new subspecies has had a heuristic benefit in elucidating patterns of geographic variation which might have otherwise gone unnoticed. It is now largely believed, as opined by

Barrowclough (1982), that looking for subspecies to describe is an innappropriate type of taxonomic work, and subspecies should be only the occasional biproduct of studies of geographic variation. Many ecologists have been alerted by subspecific names to subjects for study of adaptation to local selection pressures in widespread species. Such workers frequently find it convenient to have formal names to apply to the subjects of their investigations. Subspecies can be of interest in the context of historical biogeography in that they can (although they need not necessarily) be units of evolution. Some geographically isolated subspecies may represent "incipient species": should the selection pressures which brought about their subspecies-level differentiation continue for a sufficient period of time, speciation may occur.

As Monroe (1982) points out, Mayr's (1969) definition that a "subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species", is less than precise. The phrase "differing taxonomically" implies a degree of subjectivity, but, I believe it is still a good definition. After all, there are many instances where the biological species concept breaks down and must be applied in an arbitrary manner, yet no one would seriously suggest that we scrap the species concept! Subjectivity cannot be completely removed from taxonomic work. The judicious application of subspecies names can be appropriate where studies of geographical variation show reasonable grounds for recognizing subsets of a species.

In the absence of direct breeding evidence, relationships between phena in this study were inferred, based on holomorphological evidence with emphasis on adult structure and supplemented with some ecological and distributional data. Sympatric forms which show little or no intergradation in at least one character are considered specifically distinct. Allopatric forms which intergrade clinally over a fairly wide zone of contact are considered subspecies if the forms are sufficiently different structurally. Allopatric populations which are completely isolated geographically are considered subspecies if they differ only in color or color pattern.

STRUCTURAL AND ECOLOGICAL FEATURES OF THE NEARCTIC TAXA OF THE *C. SYLVATICA* GROUP

This section includes: (1), an analysis of adult features, including discriminant analyses of morphometric data, and characterization of the pattern of variation of qualitative characters of color and color pattern; (2), a description of immature stages and life history of *C. longilabris*; and (3), a treatment of soil associations of the two species.

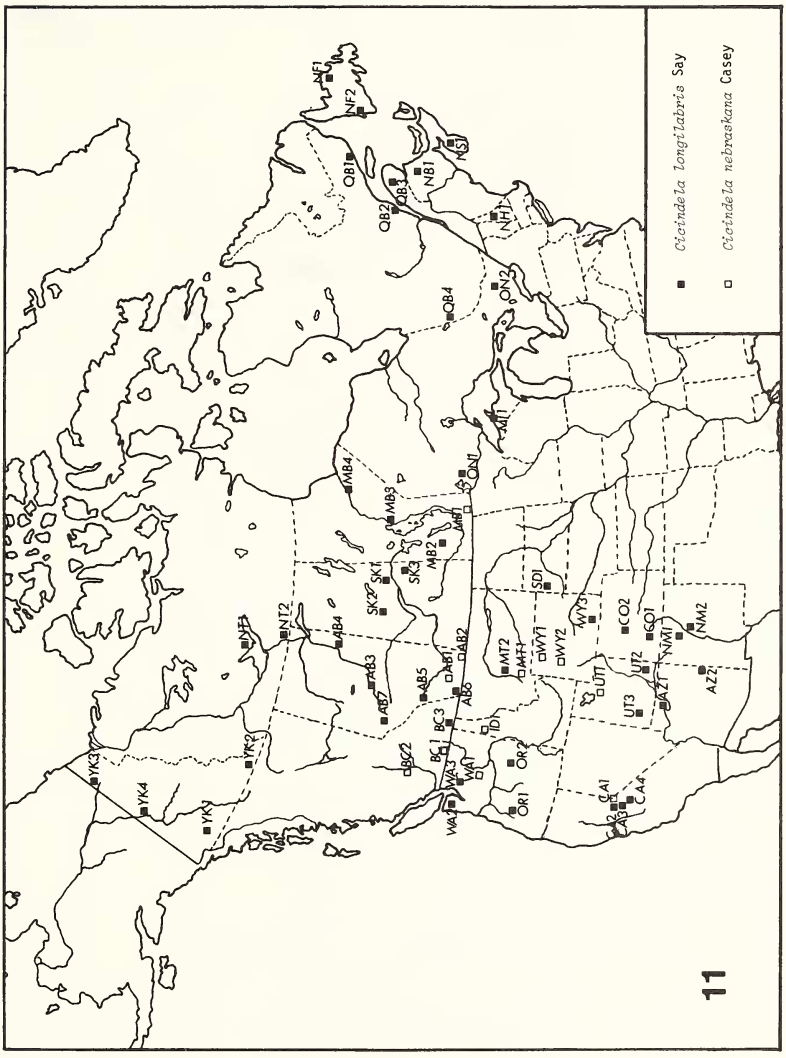


Fig. 11. Population samples used in numerical and color analysis (Table 4).

TABLE 4. Population samples of *C. longilabris* and *C. nebraskana* used in numerical and color analyses (Fig. 11).

Species	Code	Locality	N Males	N Females
C. nebraskana	AB1	Alberta: Lethbridge	11	9
	AB2	Alberta: 16 km. E. Patricia	8	3
	BC1	British Columbia: Oliver	11	21
	BC2	British Columbia: Chilcotin	15	16
	CA1	California: Tuolumne/Mono Co. Sonora Pass	11	12
	ID1	Idaho: Moscow Mountain	15	15
	MB1	Manitoba: Ninette	3	5
	MT1	Montana: Bozeman	10	16
	UT1	Utah: Lake Co. Mill Creek Canyn	3	6
	WA1	Washington: 8km. W. Cle Elum	8	6
	WY1	Wyoming: Park Co. Clay Butte	4	6
	WY2	Wyoming: Sublette Co. Lower Green River Lake	12	18
C. longilabris	AB3	Alberta: Fawcett	12	12
	AB3	Alberta: McMurray	17	6
	AB5	Alberta: 7.2 km. N. Banff	13	18
	AB6	Alberta: 20 km. W. Beaver Mines	19	16
	AB7	Alberta: Wm. A. Switzer Prov. Park 12 km. N. Hinton	4	14
	AZ1	Arizona: Kaibab Nat. Forest Kabib Lodge vicinity	10	20
	AZ2	Arizona: Apache Co. White Mtns & Escudilla Mtns. area	6	18
	BC3	British Columbia: Creston	16	14
	CA2	California: Tuolumne/Mono Co. Tioga Pass	13	15
	CA3	California: Tuolumne/Mono Co. Sonora Pass	15	15
	CA4	California: Yosemite Nat. Park Saddlebag Lake	8	24
	CO1	Colorado: Mineral Co., Creede	14	16

(continued on next page)

Table 4 (continued)

Species	Code	Locality	N Males	N Females
	CO2	Colarado: Pitkin/Lake Co., Independence Pass	17	19
	MB2	Manitoba: Riding Mtn. Nat. Park	5	3
	MB3	Manitoba: Norway House	8	7
	MB4	Manitoba: Gillam	27	34
	MI1	Michigan: Houghton Co. Oskar	18	12
	MT2	Montana: 19 km. S. Neihart	4	5
	NB1	New Brunswick: Various Localities	4	7
	NF1	Newfoundland: Gander	26	24
	NF2	Newfoundland: Harmon Field	21	10
	NH1	New Hampshire: Twin Mtn.	11	22
	NM1	New Mexico: Sandoval Co. Jemez Mtns.	10	6
	NM2	New Mexico: Bernallilo Co. Sandia Crest	7	7
	NS1	Nova Scotia: various localities	3	6
	NT1	Northwest Territories: Yellowknife	7	10
	NT2	Northwest Territories: Fort Smith	16	16
	ON1	Ontario: Kenora vicinity	16	23
	ON2	Ontario: Maynooth	–	6
	OR1	Oregon: Lost Prairie Campground Nr. Sweethome	6	11
	OR2	Oregon: Blue Mtns. Bone Springs	10	13
	QB1	Québec: Thunder River (Rivière aux Tonneres)	8	10
	QB2	Québec: Forestville	11	11
	QB3	Québec: Mont Albert	7	11
	QB4	Québec: Duparquet	15	15
	SD1	South Dakota: Black Hills Sturgis-Lead	8	11
	SK1	Saskatchewan: Torch River	13	10
	SK2	Saskatchewan: Big River	8	1
	SK3	Saskatchewan: Hudson Bay	16	6

(continued on next page)

Table 4 (continued)

Species	Code	Locality	N Males	N Females
	UT2	Utah: San Juan Co. Abajo Mtns.	6	5
	UT3	Utah: Iron Co. 5 km. S. Cedar Breaks Nat. Mon.	8	8
	WA2	Washington: Olympic Nat. Park	24	30
	WA2	Washington: Chelan Co. Stevens Pass	27	5
	WY3	Wyoming: Medicine Bow Mtns. 13 km. N. Centennial	5	6
	YK1	Yukon: Whitehorse	8	9
	YK2	Yukon: Watson Lake	5	2
	YK3	Yukon: Rampart House	3	4
	YK4	Yukon: Dawson	1	4
TOTAL			647	710

TABLE 5. Canonical discriminant functions evaluated at group centroids for discriminant analyses of *C. longilabris* and *C. nebraskana*.

Test	Sex	Group	Function 1	Sign.	Function 2	Sign.	Function 3	Sign.
1	M	NF1	-1.47603		0.34675		0.14078	
		NF2	0.42626		-1.17008		-0.38365	
		QB3	1.76261		-0.26151		1.36885	
		QB2	1.55336	0.0000	1.58061	0.0001	-0.47121	0.796
2	F	NF1	-1.03027		0.26421		0.23094	
		NF2	0.48235		0.32265		-1.52325	
		QB3	0.45092		-1.7608		0.07403	
		QB2	2.29503	0.0000	0.65092	0.0001	0.59693	0.0087
3	M	Boreal	-0.67659		0.14247			
		Pacific	1.02706		0.48910			
		Rocky Mtn.	0.39649	0.0000	-0.91121	0.0000		
4	F	Boreal	-0.68318		0.30761			
		Pacific	1.19467		0.45284			
		Rocky Mtn.	0.12659	0.0000	-1.00810	0.0000		

(continued on next page)

Table 5 (continued)

Test	Sex	Group	Function 1	Sign.	Function 2	Sign.	Function 3	Sign.
5	M	*C. nebraskana* W.	0.94882					
		C. nebraskana E.	-1.18602	0.0000				
6	F	*C. nebraskana* W.	0.88205					
		C. nebraskana E.	-1.15877	0.0000				
7	M	*C. nebraskana*	-2.02870					
		C. longilabris	0.40574	0.0000				
8	F	*C. nebraskana*	1.87920					
		C. longilabris	-0.42643	0.0000				

TABLE 6. Test 1, F statistics* and associated significance levels+ between groups of males of *C. longilabris* from NF1, NF2, QB2 and QB3 populations. Each F statistic has 11 and 51 degrees of freedom.

Group	NF1	NF2	QB2
NF2	5.4696* 0.0000+		
QB2	6.5061 0.0000	4.8526 0.0000	
QB3	5.1840 0.0000	2.2677 0.0243	2.2184 0.0276

TABLE 7. Test 2, F statistics* and associated significance levels+ between groups of females of *C. longilabris* from NF1, NF2, QB2 and QB3 populations. Each F statistic has 11 and 52 degrees of freedom.

Group	NF1	NF2	QB2
NF2	3.1630* 0.0024+		
QB2	7.1868 0.0000	3.1506 0.0025	
QB3	4.0046 0.0003	2.7531 0.0069	3.9801 0.0003

TABLE 8. Test 3, F statistics* and associated significance levels+ between groups of males from the combined population samples of *C. longilabris* from the Rocky Mountain States, Pacific Region and the Boreal Region.
Each F statistic has 12 and 431 degrees of freedom.

GROUP	BOREAL ZONE	PACIFIC REGION
Pacific Region	18.885* 0.0000+	
Rocky Mtn. Region	12.662 0.0000	10.140 0.0000

TABLE 9. Test 4, F statistics* and associated significance levels+ between groups of females from the combined population samples of *C. longilabris* from the Rocky Mountain States, Pacific Region and the Boreal Region.
Each F statistic has 12 and 464 degrees of freedom.

GROUP	BOREAL ZONE	PACIFIC REGION
Pacific Region	22.872* 0.0000+	
Rocky Mtn. Region	15.807 0.0000	16.323 0.0000

Analysis of adult features

Discriminant analysis.— Figure 11 and Table 4 indicate the population samples used in these analyses. Table 5 indicates the canonical discriminant functions derived in each of the tests and Tables 6 to 9 present F statistics and associated significance levels for comparisons among groups. Table 10 indicates variables selected by the discriminant program in each of these tests.

Discriminant analysis tests 1 and 2 (Tables 5, 6 and 7) were conducted to investigate variation among population samples from Gander, Nfld. (NF1), Harmon Field, Nfld.(NF2), Thunder River, Québec (QB2) and Mont Albert, Québec (QB3) (Fig. 11). This was done to seek significant metric differences between Newfoundland and mainland populations, to corroborate Leng's (1918) designation of the formal name *C. l. novaterrae*, applied to the island populations based on an increased frequency of green colored individuals. In test 1 for males, two discriminant functions were derived which dealt with a significant amount of variation (Table 5). Function 1 scored the two Québec populations close together, with NF2 having an intermediate value and NF1 scored farthest from the Québec populations. Function 2 scored NF1 and QB3 closer together near the mid range of the scale, with QB3 and NF2 farthest apart at either end of the range of values. In both functions, measurements of the labrum and pronotum contributed most to the functions (Table 10). Males from Newfoundland were found to have a larger labrum and a larger pronotum. These differences seem to reflect a difference in body size, those specimens on the island being larger, on average. It is a commonly occurring phenomenon, for island populations of animals to be different in size. Freitag (1965) showed that specimens of *Cicindela oregona* on the Queen Charlotte Islands are larger, on average than mainland specimens, and Lindroth (1963: 88) indicated that a number of species of carabid beetles are noticeably larger in body size on the island of Newfoundland than are their mainland populations.

The F statistics and associated significance levels between groups (Table 6) indicate a discordant pattern of variation. Males from NF1 are different from QB2 and QB3 at a significance level beyond 0.0001, whereas NF2 males are not significantly different from QB3 males at a 0.01 level. NF1 males and NF2 males differ from each other significantly beyond the 0.0001 level. This greater statistical difference between populations from Newfoundland than between NF2 and QB3 seem to refute subspecific status for Newfoundland populations, based on morphometric characters.

Test 2 (Table 5), with female specimens also produced two functions with a significant amount of variation (at or beyond the 0.0001 level). Function 1 separates most strongly between NF1 and QB2 at opposite ends of the range of values, with NF2 and QB3 having very similar scores, intermediate on the scale. Function 2 scores QB2, NF1 and NF2 close together with QB3 distinctly separate from the other three. Femur length and tibia length are the variables contributing the greatest amount of variation to Functions 1 and 2 for females of these four populations. The

multivariate F statistics and associated significance levels for test 2 (Table 7) indicate that females of NF2 do not differ from those of QB2 and QB3 significantly at the 0.001 level. The F statistics and significance level between NF1 and NF2 is comparable to that between the NF2 and Quebec populations. These differences based on morphometric characters do not warrant subspecific distinction between the populations on Newfoundland and those of the mainland.

Discriminant tests 3 and 4 compared three large groupings of population samples of *C. longilabris*: (1), grouped populations of the Rocky Mountain states from Montana to Arizona and New Mexico (MT2, SD1, WY3, CO1, CO2, UT2, UT3, AZ1, AZ2, NM1 and NM2)(Table 4, Fig. 11); (2), grouped populations of the Cascade and Sierra Nevada Mountains from southern British Columbia to east central California (BC3, WA2, WA3, OR1, OR2, CA2, CA3, CA4)(Table 4, Fig. 11); and (3), the nominal form from across the boreal zone in its broadest sense in the northern part of the continent (all remaining population samples, Table 4, Fig. 11).

In test 3, comparing male specimens, two functions were derived with a significant amount of variation (significant beyond the 0.0001 level, Table 5). Table 8 for test 3 indicates multivariate F figures between any two of these groups significant beyond the 0.0001 level. Test 4, comparing female specimens, produced very similar results. Two highly significant discriminant functions were produced (Table 5). One function set the Pacific form apart from the other two and the second function separated the Rocky Mountain group from the Pacific and Boreal forms. Table 9 shows that any two-group comparison among these three, has an F statistic that is significant beyond the 0.0001 level. Both male and female specimens show highly significant statistical differences among these groups, beyond the minimum significance level (0.0001) here chosen for taxonomic purposes.

The variables contributing most to the discrimination among these three groups were pronotal width (pw), pronotal length (pl), per cent of elytral surface covered with maculations (prct), head width (hw), length of mesothoracic tibia (tl) and elytral width (ew)(Table 10). A one-way analysis of variance was performed to investigate the statistical differences in each of these measurements. For males, all three groups were statistically different from each other in pw ($F=27.958$, $p=0.0001$, sign. at 0.05 by Scheffe's procedure) and hw ($F=25.710$, $p=0.001$, sign. at 0.05 by Scheffe's procedure). For both of these variables males of the Boreal group measured the largest and the Pacific group measured smallest. Similarly for females, a one-way analysis of variance (ANOVA) showed that each of the groups differs from the others based on the variables pw ($F=57.793$, $p=0.0001$, sign. at 0.05 by Scheffe's procedure) and hw ($F=52.201$, $p=0.0001$, sign. at 0.05 by Scheffe's procedure). For both variables, females of the Boreal form had the largest average measurement and the Pacific form was the smallest of the three. These statistics probably reflect the overall size differences, with the nominate form largest in body size, the Rocky Mountain form smaller, and the Pacific form smallest.

The Boreal form has a proportionately shorter, wider pronotum than the other two groups evidenced by the statistical difference in the variable pl/pw (ANOVA, Males: F=42.165, p=0.0001, sign. at 0.05 by Scheffe's procedure; Females: F=36.908, p=0.0001, sign. at 0.005 by Scheffe's procedure).

Per cent of the elytral surface covered with maculations was another discriminating variable which shows statistical differences among the groups. An ANOVA of male specimens confirmed that the Boreal form is less maculate than the other two groups (F=43.175, p=0.0001, sign. at 0.05 by Scheffe's procedure). The same test with female specimens also confirmed that the Boreal form is least maculate, the Rocky Mountain group more so, and the Pacific group most maculate, on average (F=55.577, p=0.0001, sign. at 0.05 by Scheffe's procedure).

Discriminant tests 5 and 6 compared population samples of *C. nebraskana* from east of the Rocky Mountains with those west of the continental divide. Leffler (1979) in studying tiger beetles of the Pacific Northwest recognized two subspecies, *C. n. nebraskana* from east of the divide and *C. n. chamberlaini* from west of the divide, based primarily on a statistical difference in head width: the eastern populations having narrowest heads with intermediate populations occurring near the divide in eastern Idaho and northwestern Wyoming. Test 5 (Table 5) for male specimens, produced a discriminant function which separated between the eastern and western populations significant beyond the 0.0001 level. The variables contributing most to the discriminant function were, in order of importance, fl and el (Table 10). Hw was not selected in this analysis. Test 6 using female specimens also separated between the groups, with a multivariate F ratio of 14.166, significant beyond the 0.0001 level. In this discriminant function the variables contributing most to the variation were, in order of importance, fl and hw.

Using an ANOVA, with the probability of a type one error set at 0.01, for both males and females, the western group of *C. nebraskana* had significantly longer mesofemora, on average and larger elytra than the eastern populations. No differences in other measurements significant at the 0.05 level were found between the eastern and western populations of *C. nebraskana*.

Discriminant tests 7 and 8 compared *C. longilabris* with *C. nebraskana*. As Table 5 indicates, for test 7, comparing male specimens, a discriminant function was derived which separated the two groups very well. The multivariate F ratio was 39.988, significant beyond the 0.0001 level. The variables which contributed most to the discriminant functions were ll, lw, ll/lw, prct, hw/pw, lcol, and ls2 (Table 10).

The discriminant function derived in test 8 between females of the two species, was also highly significant (Table 5). The multivariate F ratio was 50.403, significant beyond the 0.0001 level. The variables most effective in separating the females of the forms were prct, lw, lcol, ll/lw, pw, ls2, and osr (Table 10).

In summary, using an ANOVA with probability of a type one error at 0.001, males and females of *C. longilabris*, as compared to those of *C. nebraskana*, have significantly longer and wider labra, have proportionately longer labra relative to

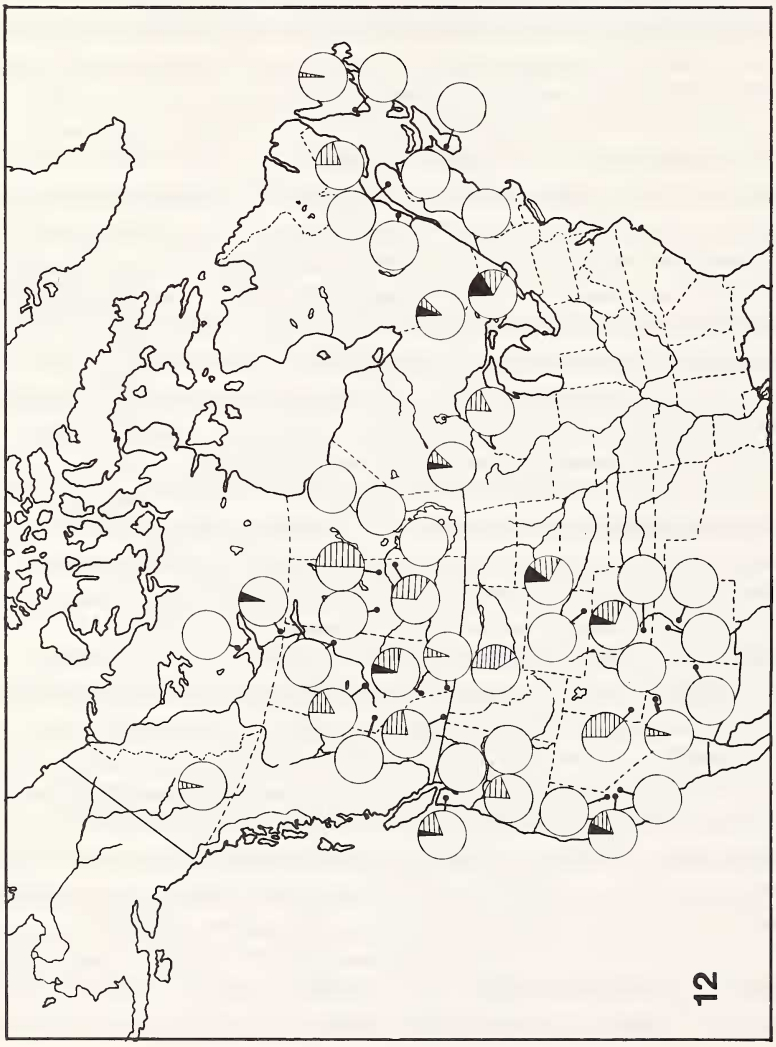


Fig. 12. Relative frequency of color states of the female labrum in population samples of *C. longilabris* Say: white, light colored labrum; horizontal lines, labrum partly darkened or intermediate in color; black, labrum black, or nearly so. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon samples are combined for this purpose.

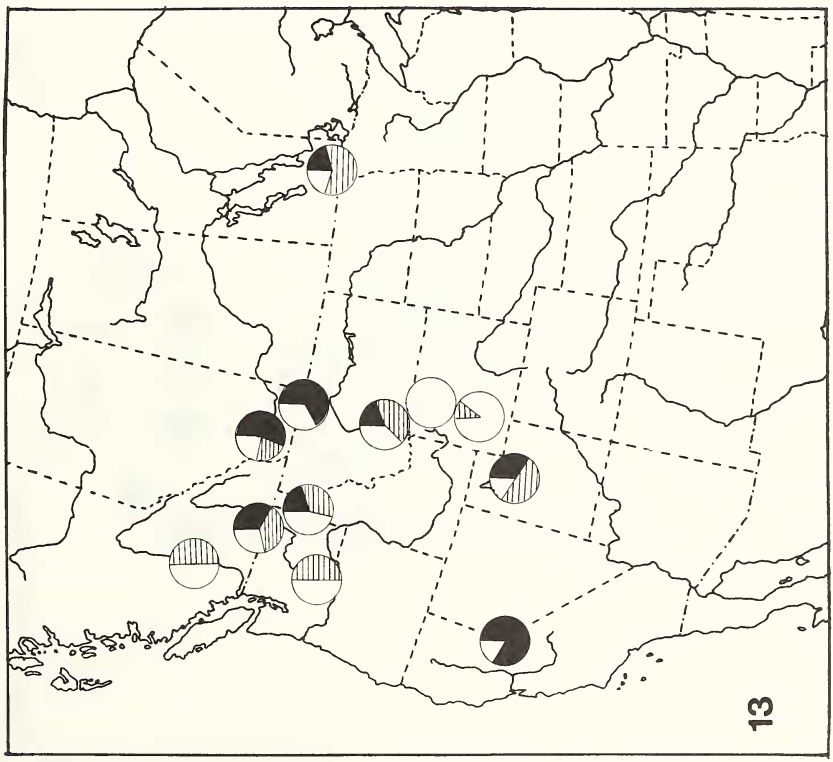


Fig. 13. Relative frequency of color states of the female labrum in population samples of *C. nebraskana* Casey: white, light colored labrum; horizontal lines, intermediate colored or mottled; black, black or nearly so. Population samples are indicated in Table 4 and Figure 11.

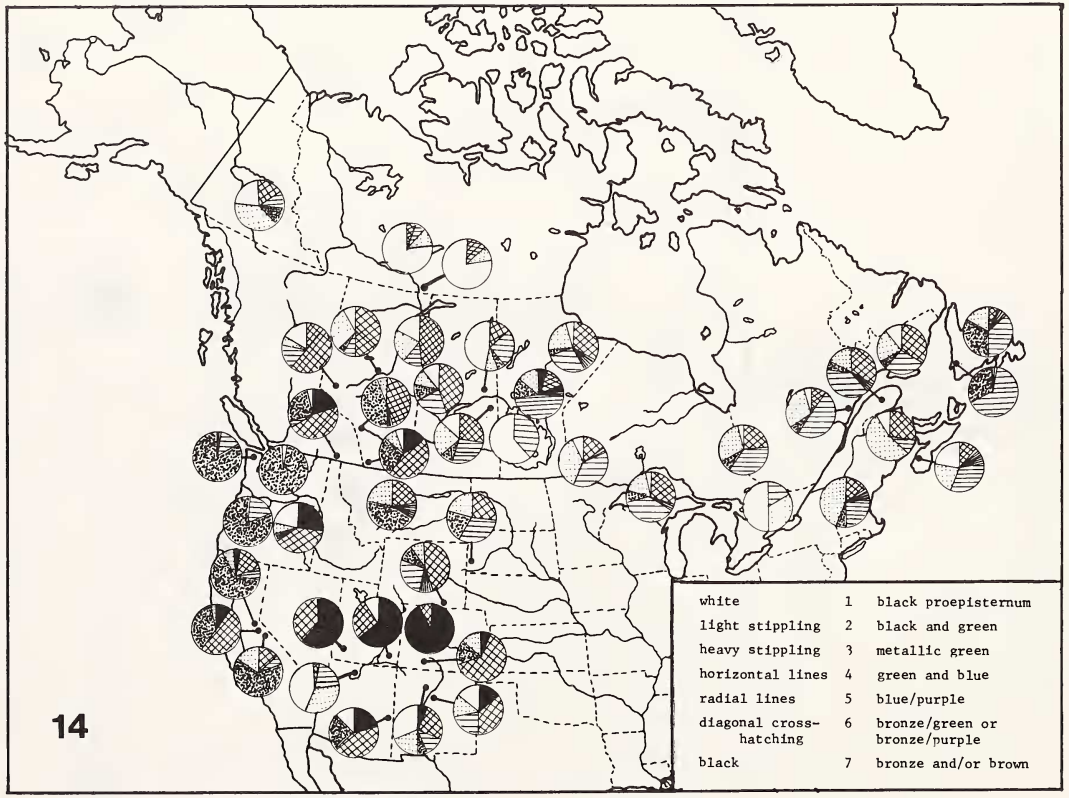


Fig. 14. Relative frequency of color states of the proepisternum in population samples of *C. longilabris* Say. Color states are described in Table 2. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon samples are combined.

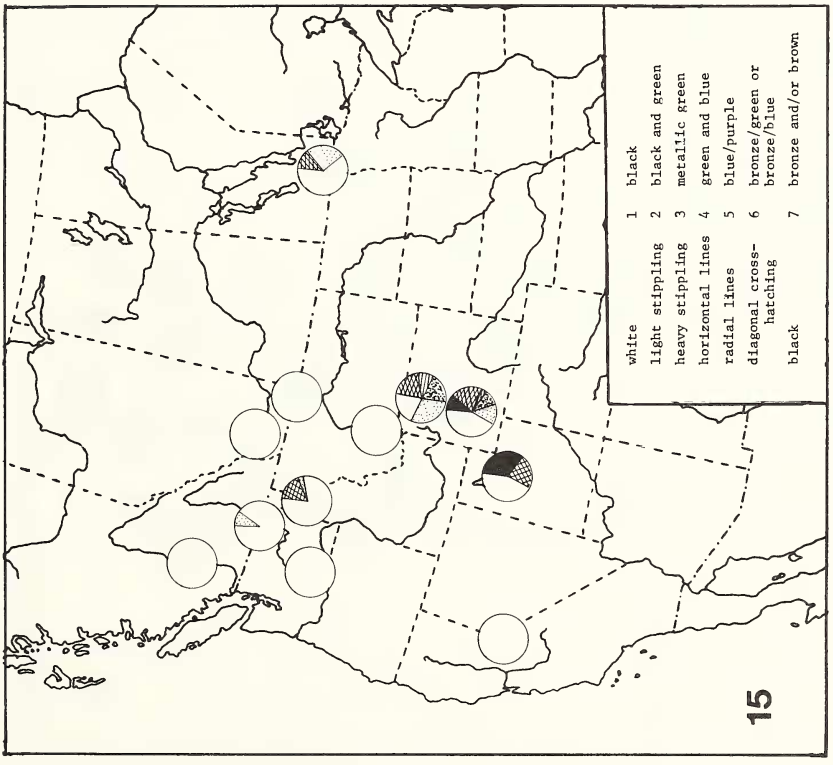


Fig 15. Relative frequency of color states of the proepisternum in population samples of *C. nebraskana* Casey. Color states are described in Table 2. Population samples are indicated in Table 4 and Figure 11.

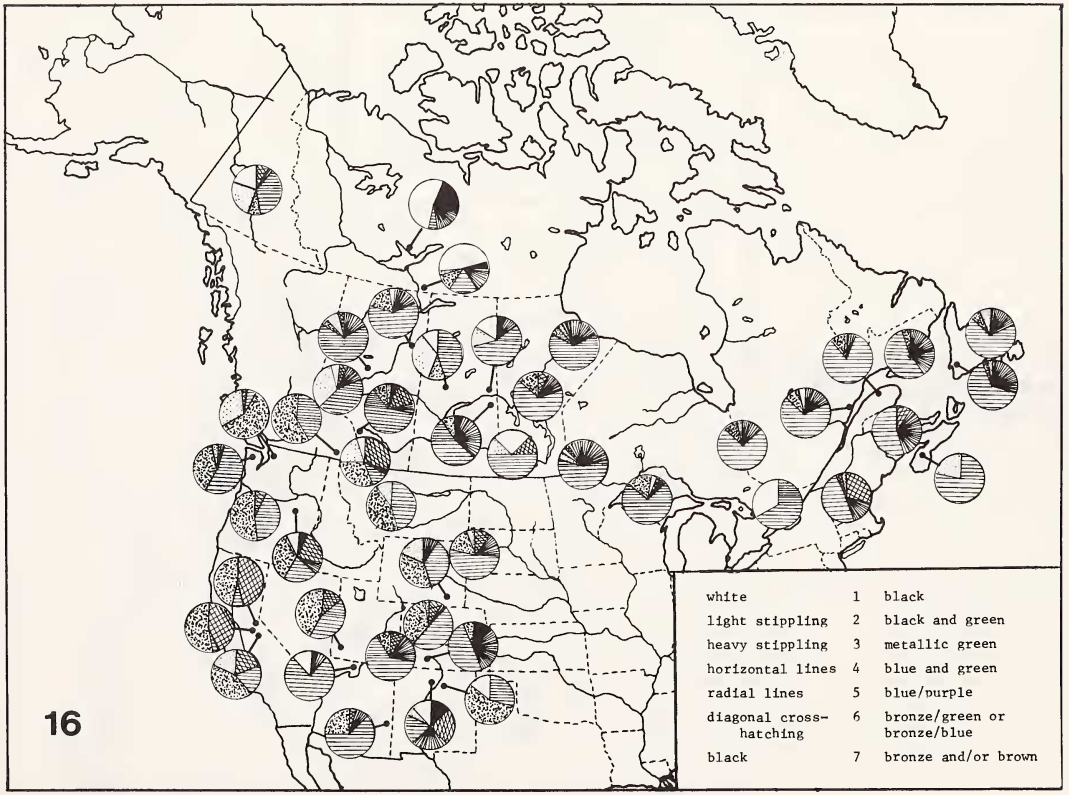


Fig. 16. Relative frequency of color states of the abdomen in population samples of *C. longilabris* Say. Color states are described in Table 3. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples are combined.

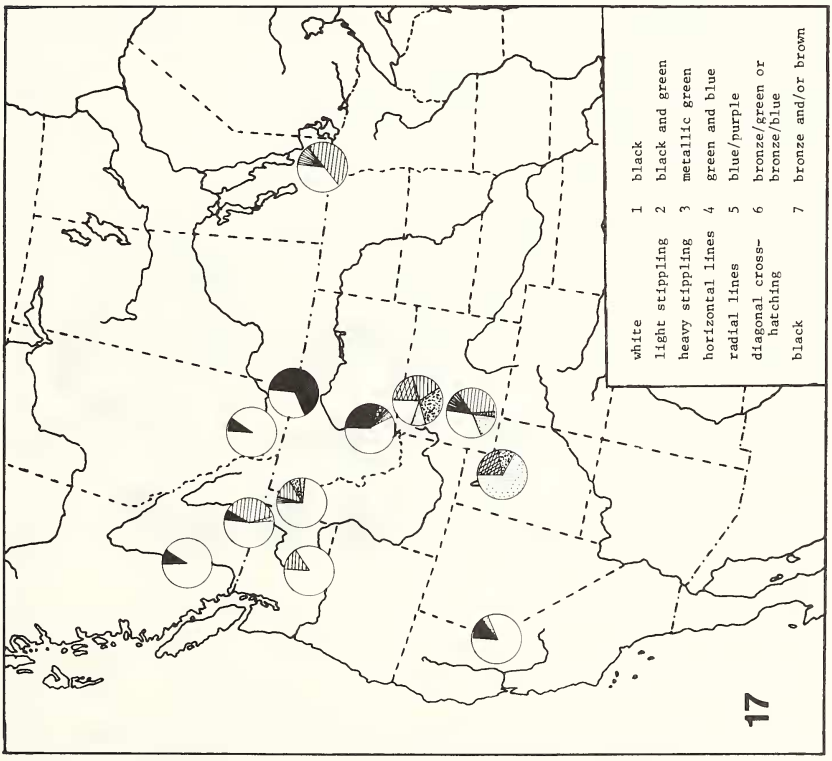


Fig. 17. Relative frequency of color states of the abdomen in population samples of *C. nebraskana* Casey. Color states are described in Table 3. Population samples are indicated in Table 4 and Figure 11.

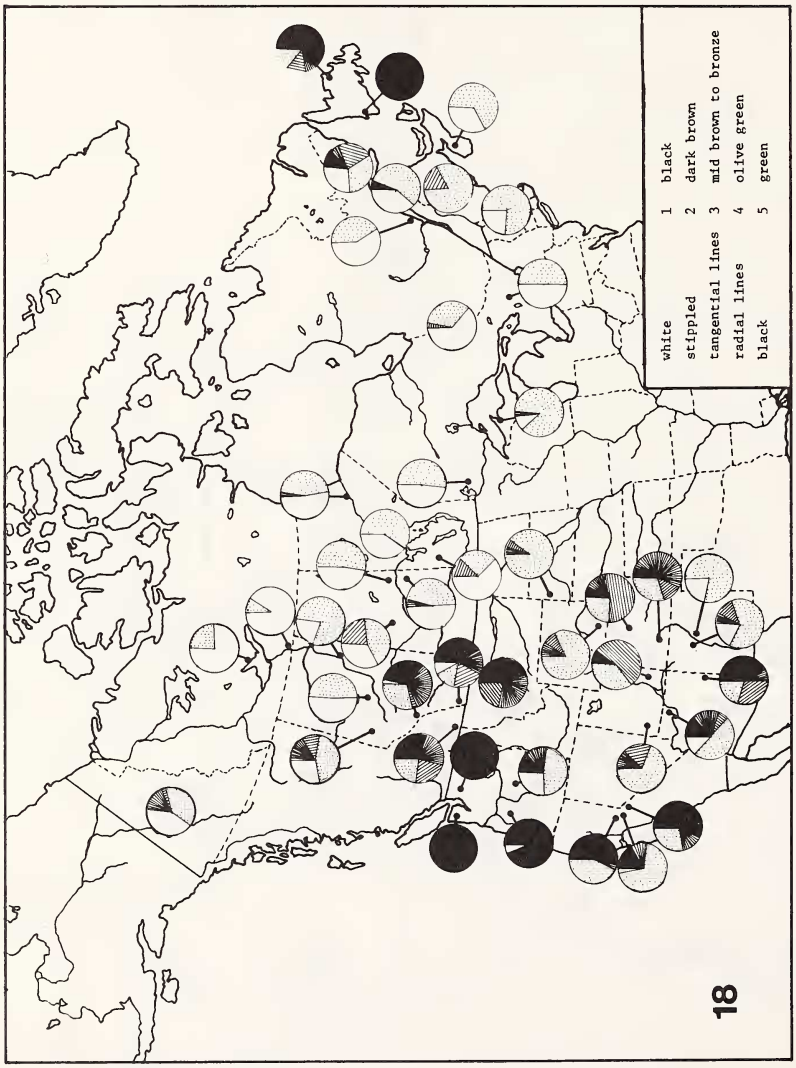


Fig. 18. Relative frequency of color states of the elytra in population samples of *C. longilabris* Say. Color states are described in Table 1. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples are combined.

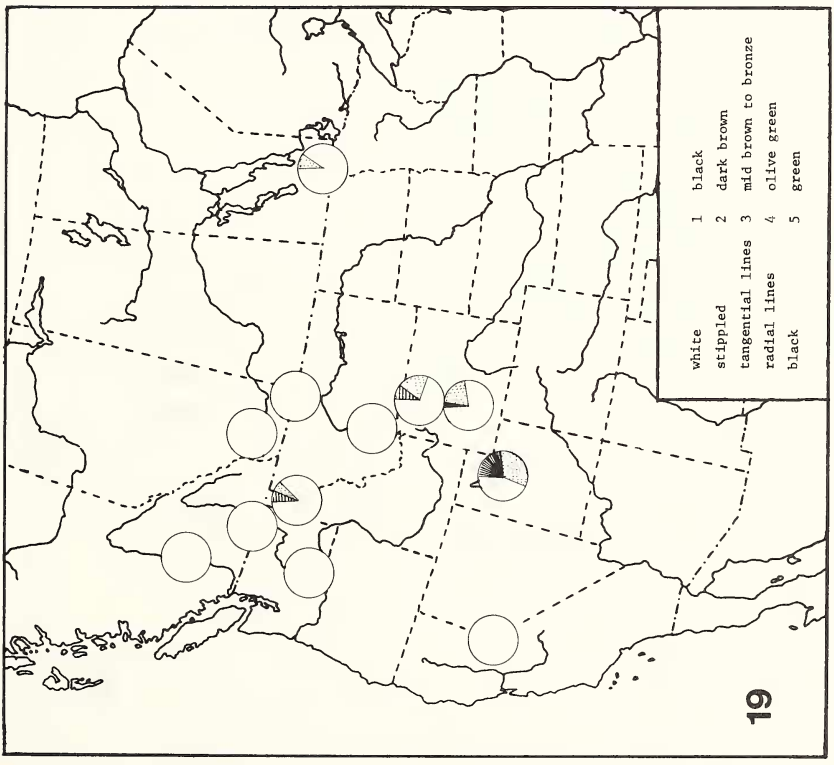


Fig. 19. Relative frequency of color states of the elytra in population samples of *C. nebraskana* Casey. Color states are described in Table 1. Population samples are indicated in Table 4 and Figure 11.

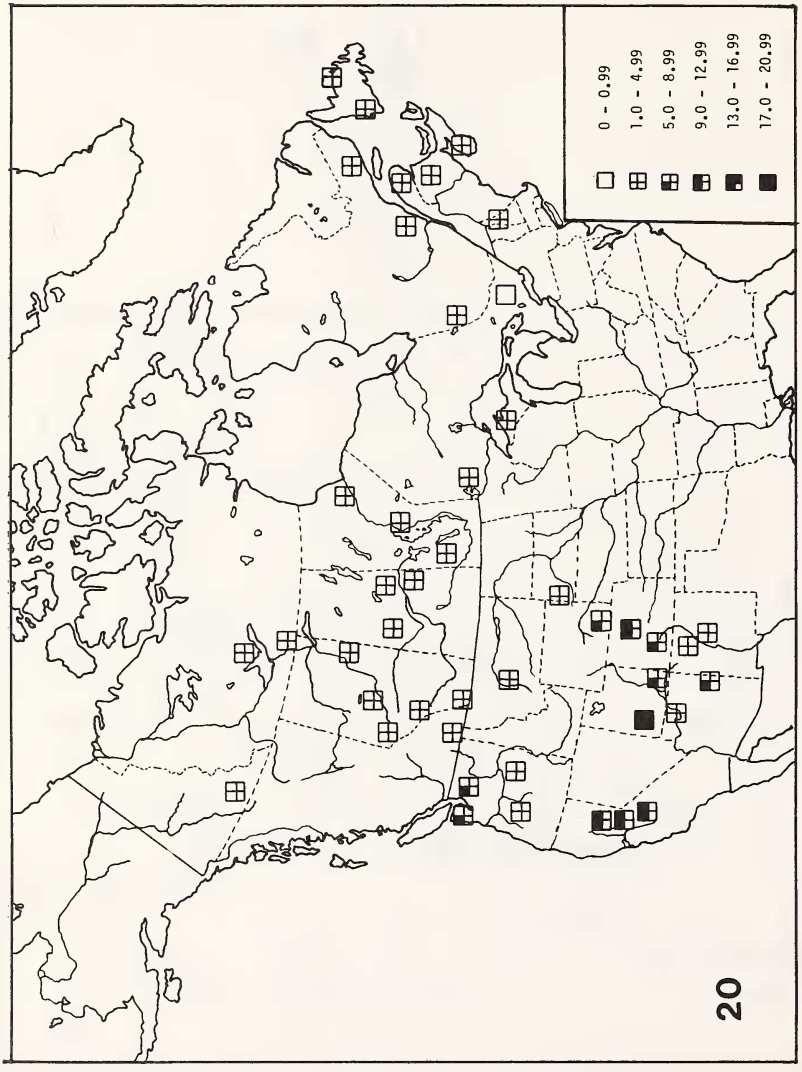


Fig. 20. Weighted mean percentage of surface area of elytra covered with maculations (Fig. 7), for population samples of *C. longilabris* Say. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples are combined.

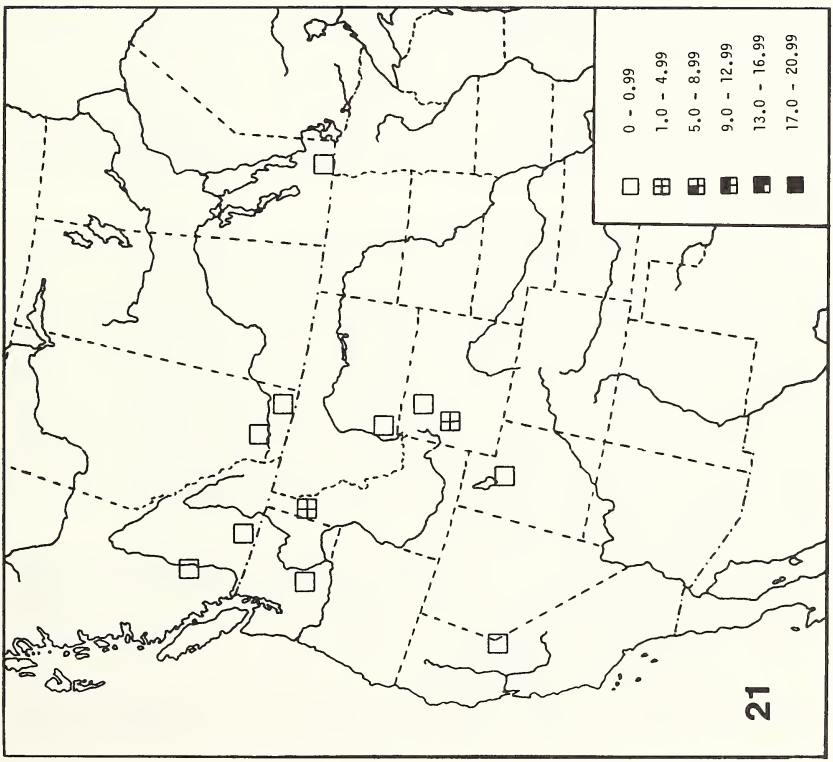


Fig. 21. Weighted mean percentage of surface area of elytra covered with maculations (Fig. 7), for population samples of *C. nebraskana* Casey. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11.

labral width, are more maculate, and have proportionately wider heads, in relation to pronotal width. Males and females of *C. nebraskana* have significantly more non-sensory setae on the scape of the antenna (Fig. 3) than *C. longilabris,* but individuals could not be identified on that basis.

Color and pattern of markings.— Figure 12 presents the frequency of occurrence of three categories of labrum color for females of each population of *C. longilabris.* In most samples, all females had light colored labra, in some populations a significant fraction of females exhibited labra intermediate in color, mottled, or darkened along the outside edge and midrib. In a small number of population samples a small fraction of females had dark colored labra. A geographic pattern to the variation in this character in *C. longilabris* was not identified.

The frequency of occurrence of color character states of the female labrum is highly variable among populations of *C. nebraskana* (Fig. 13). In samples from southern Alberta (AB1, AB2)(Table 4, Fig. 11), and eastern California (CA1), the dark colored labrum predominates. In the Wyoming populations (WY1, WY2) most females have light colored labra, and in other populations studied the three character states are represented in varied frequencies between the two extremes. There appears to be no pattern to the variation in this character in *C. nebraskana.* Overall, among *C. nebraskana* females 44.8% had light colored labra, 30.6% were intermediate in color, and 24.6 % were black (total, n=134). In contrast, among *C. longilabris* females, labra were light in 90.3%, intermediate in character in 8.2% and black in color in 1.5% of specimens (n=586).

Among male specimens of *C. nebraskana,* 82.6% had light labra, 15.6% intermediate, and 1.8% black (n=109), and among *C. longilabris* males the corresponding figures were 97.6% light labra, 1.8% intermediate, and 0.6% dark (n=538).

Figure 14 shows the frequency of occurrence of colors of the proepisternum of *C. longilabris.* This character varies across the range of the species, but in most populations, specimens with green and black, green, green and blue, or bronze and green colored proepisterna (character states 2–7, Table 2), make up the largest fraction of the samples. Figure 15 shows the frequency of proepisternal color states in population samples of *C. nebraskana.* In this species the proepisterna in most of the populations are black in color, with notable exceptions being the Wyoming populations (WY1 and WY2) and the northern Utah population (UT1), in each of which specimens with bronze colored proepisterna (character states 6, 7, Fig. 15) make up a large fraction of the sample.

Figure 16 presents frequency of occurrence of colors on the ventral surface of the abdomen in *C. longilabris* This character varies throughout the species, but metallic greens and mixtures of metallic greens, blues and bronze color (character states 3, 4, 6, Table 3) predominate in most populations.

In contrast, Figure 17 shows the frequency of occurrence of various colors of the venter of the abdomen in specimens of *C. nebraskana.* In most population samples,

TABLE 10. Variables (as described in the Materials and Methods section) selected in discriminant analysis of *Cicindela longilabris/nebraskana*. The 'X' indicates variables that failed the minimum tolerance test (minimum tolerance = 0.001). The '+' indicates variables selected to maximize the Mahalanobis Distance between groups.

Test	Sex	hw	ll	lw	lcol	ls1	ls2	ls3	ls4	ss1	ssr	os1	osr	pw	pl	fl	tl	el	ew	prct	ll/lw	pl/pw	hw/pw	fl/tl	ew/el	fl/el
1	M		+	+		+	+							+	+		+			+	+	+			+	
2	F		+	X			+	+						+		+	+			+	+			+		
3	M	+	+				+		+			+			+	+			+	+	+					
4	F	+		+			+				+	+	+		+	+			+	+			+			
5	M				+	+	+		+				+			+			+						+	
6	F	+	+			+				+		+			+	+										
7	M		+	+	+		+			+	+		+					+			+	+				
8	F			+	+		+		+	+	+		+	+						+	+					+

TABLE 11. Weighted mean values of characters prct, hl, mb, al for samples of *C. nebraskana* and *C. longilabris*. Characters are defined in the Materials and Methods section and indicated in Figs. 4, 5, 6, and 7.
Locality codes are defined in Table 4 and illustrated in Figure 11.

	Population	prct	hl	mb	al
C. nebraskana	AB1	0.5	0.00	0.05	0.00
	AB2	0.5	0.09	0.09	0.00
	BC1	0.6	0.00	1.22	0.13
	BC2	0.9	0.55	0.71	0.13
	CA1	0.6	0.00	0.96	0.04
	ID1	1.2	0.03	1.40	0.26
	MB1	0.7	0.38	1.00	0.38
	MT1	0.5	0.04	0.27	0.00
	UT1	0.7	0.00	0.89	0.11
	WA1	0.7	0.64	1.36	0.14
	WY1	0.5	0.10	0.10	0.00
	WY2	1.6	0.20	1.80	0.13
C. longilabris	AB3	2.9	2.21	1.54	0.75
	AB4	4.6	2.87	1.83	1.13
	AB5	4.5	2.13	2.36	0.94
	AB6	4.0	1.94	2.06	1.06
	AB7	2.7	2.44	1.78	0.89
	AZ1	4.1	2.20	2.17	1.67
	AZ2	5.9	2.79	3.54	1.33
	BC3	4.8	1.97	2.33	1.13
	CA2	11.2	3.86	4.75	2.57
	CA3	10.2	3.87	3.23	3.00
	CA4	10.7	4.00	4.25	2.47
	CO1	8.5	2.53	3.53	3.07
	CO2	11.4	3.36	4.64	3.50
	MB2	1.8	1.50	1.25	0.38
	MB3	3.2	2.5	1.7	0.7
	MB4	3.2	2.53	1.8	0.82
	MI1	3.2	2.70	1.43	0.90
	MT2	3.7	2.40	2.44	1.10
	NB1	3.1	2.3	1.6	1.0
	NF1	4.3	2.82	1.98	0.98
	NF2	4.8	3.00	2.00	1.13
	NH1	3.2	2.36	1.70	0.85
	NM1	1.7	0.75	1.38	0.50
	NM2	1.0	0.29	0.57	0.21

(continued on next page)

Table 11 (continued)

Population	prct	hl	mb	al
NS1	1.4	2.90	1.90	1.10
NT1	3.4	2.35	1.65	0.94
NT2	3.6	2.38	1.88	0.75
ON1	1.7	1.82	1.39	0.67
ON2	0.8	1.33	0.67	0.17
OR1	2.0	0.59	3.77	1.06
OR2	1.0	0.13	1.87	0.22
QB1	4.8	3.11	2.0	1.06
QB2	3.4	2.82	1.73	0.82
QB3	3.0	2.17	1.78	0.94
QB4	2.8	2.43	1.63	0.87
SD1	2.6	1.32	1.47	0.63
SK1	3.4	2.34	1.74	0.74
SK2	2.7	2.44	1.44	0.56
SK3	3.1	1.91	1.68	0.82
UT2	9.1	3.36	3.36	2.27
UT3	18.8	5.00	6.00	4.06
WA2	7.9	3.80	4.3	2.28
WA3	5.5	3.13	3.69	1.81
WY3	5.8	3.63	3.36	2.09
YK1–4	3.2	2.69	1.86	1.22

black (character state 1, Table 3) is the ventral color in the majority of specimens, with blue and purple (character state 5) and bronze (states 6, 7), comprising large fractions of some of the samples. The UT1 sample is peculiar in having a large number of specimens with black and green abdominal coloring (character state 2, Fig. 17).

Figure 18 shows the frequency of occurrence of colors of the elytra of *C. longilabris*. This character is highly variable throughout the range of the species. The blue-green and dark blue color (states 6 and 7, Table 1) occurred so rarely that they did not appear as a fraction of any of the sampled populations.

Green specimens predominate in the Newfoundland populations of *C. longilabris* (Fig. 18). The mainland specimens across eastern North America are almost all black or dark brown in dorsal elytral coloration. In the western part of the continent elytral color is more variable. In the Rocky Mountains of the western United States dark brown, bronze, and olive green (character states 2, 3, and 4) specimens predominate and in the Pacific region from California to Washington State, bright

green colored specimens are most numerous. In *C. nebraskana* (Fig. 19), black colored specimens are in the overwhelming majority with dark brown and bronze elytra occurring in small fractions of the populations.

Figures 20 and 21 show the average percentage of the elytral surface covered with maculations (Fig. 7), in *C. longilabris* and *C. nebraskana*, respectively. In the former species (Fig. 20), most of the specimens of the Boreal zone have an average of between 1 and 5 per cent of their elytral surface covered with maculations. This percentage increases greatly in specimens of some populations of the Pacific and Rocky Mountain regions of the United States.

In *C. nebraskana* (Fig. 21), most of the specimens have an average of less than one per cent of the elytral surface area covered with maculations. The exceptions are the ID1 and WY2 samples which have an average of 1.2 and 1.6 per cent, respectively, of their elytral surfaces covered with light markings.

Figures 22–27 and Table 11 present weighted mean values of characters of the elytral markings for population samples of *C. longilabris* and *C. nebraskana*. Figure 22 presents weighted mean character values of the humeral lunule (Figs. 6, 8) for population samples of *C. longilabris*. In most populations of this species the humeral lunule is present as one or two distinct dots or as a complete lunule (Fig. 8). Figure 23 presents the weighted mean character values of the humeral lunule for samples of *C. nebraskana*. In all samples of this species, the humeral lunule is lacking from the majority of specimens.

Figure 24 presents the weighted mean character values of the middle band (Figs. 6, 8) for *C. longilabris*. In most population samples from the Boreal zone, the middle band is either indistinctly present (state 1, Fig. 9) or complete, but quite thin (state 2, Fig. 9). The middle band is more developed in the southern Rocky Mountain region and in the Pacific coast states. Figure 25 presents weighted mean character values of the middle band (Fig. 9) for samples of *C. nebraskana*. In a majority of the populations the middle band is lacking completely in most specimens. In BC1, WA1, ID1, WY2 and MB1 (Fig. 11) the middle band is either incompletely present or is present as a thin line (states 1 and 2, Fig. 9) in most specimens.

Figure 26 presents weighted mean character values of the apical lunule of samples of *C. longilabris*. In some populations in the Atlantic region of Canada (QB1, NF2, NB1, NS1, Fig. 11), the apical lunule is typically a dot of varying size (states 1–2, Fig. 10). In most of the samples from across the Boreal zone the apical lunule is missing (state 0, Fig. 10), or is present as a dot of varying size (states 1, 2, Fig. 10). The apical lunule is more developed in many populations of the southern Rocky Mountains and Pacific regions, but is quite variable between populations.

Figure 27 shows weighted mean character values for the apical lunule of samples of *C. nebraskana* In all sampled populations of this species the apical lunule is lacking from the majority of specimens but present as a small dot (character state 1, Fig. 11) in a few specimens.

Larvae and Life History Data

Larvae of Cicindela longilabris.— Leffler (1979) described the third instar larva of *C. nebraskana* and a single second instar larval specimen of *C. longilabris* from an area of hybridization between the Rocky Mountain form, *C. l. laurentii* and the Pacific Coast form, *C. l. perviridis.*

As descriptions of larvae have in the past been based on the third instar (Hamilton, 1925; Willis, 1967), and some characters in these descriptions vary between instars of a species, the following description is based on the third instar, with differences among the three instars noted, where applicable. The format used for the descriptions of the larvae follows that of Hamilton (1925) and Willis (1967), to facilitate comparisons among species.

Material.— Twelve third instar specimens, twelve second instar specimens, and five first instar specimens were reared from mating of captive adults of *C. l. longilabris* collected near Thunder Bay, Ontario.

Description.— *Color*: Head, pronotum and clypeus bronze-black with some metallic reflections varying from green to cupreous to bronzy in some specimens; labrum black or very nearly so in second and third instars, bronze in first instars; mandibles rufous basally to black in distal portion in second and third instars, in first instars mandibles are light brown proximally to dark brown distally; antennae dark brown to black; maxillae rufous to medium brown in second and third instars, light brown in first instars, with apical segments of palpus and galea dark brown-black in many individuals of all instars; genae rufous posteriorly to dark brown or black anteriorly; mesonotum grayish brown anteriorly to light brown posteriorly; metanotum slightly lighter brown than mesonotum; legs light brown in some individuals to dark brown in others; sclerotized areas on abdomen yellowish brown in second and third instars, almost transparent in first instars; setae on head and pronotal surface brown, lighter brown in first instars, some white setae around lateral margins of pronotum; setae on remainder of body brown in second and third instars, very light brown in first instars. *Head*: Diameter of stemma I approximately equal to diameter of stemma II and approximately equal to interstemmatal distance (slightly variable); frontoclypeolabral area approximately as wide as long, or very nearly so (somewhat variable); U-shaped ridge on caudal part of frons with two setae; antennomere 4 approximately 0.7 times length of antennomere 3, antennomere 3 about 0.6 times as long as antennomere 2; antennomere 1 approximately 0.8 times length of antennomere 2; antennomere 1 with eight setae in third instar, five or six setae in second instar, zero setae in first instar; antennomere 2 with eight or nine setae in third instar, five to seven setae in second instar, two setae in first instar; antennomere 3 with two setae; antennomere 4 with two or three obvious setae and one to three minute setae in all instars; mesal edge of maxillary galeomere 1 with one seta in first instar, two setae in second instar and three setae in third instar; galeomere 2 with five setae; maxillary palpi three segmented, palpomere 2 with two setae, basal and distal palpomeres lacking setae; labial palpomere 1 with three small ventrodistal spines flanked on each side by one or two setae in second and third instars, flanking setae lacking in first instars; labial palpomere 2 with one seta; ligula usually with four setae, five in some individuals; labio-stipites with two long distinct setae and two minute setae (Figs 28, 29). *Pronotum*: Cephalolateral angles projecting as far anteriorly as mesal edge; lateral margins slightly carinate; disc with six to eight setae (seven in most individuals). (Fig. 28). *Abdomen*: Sclerotized areas distinct; secondary setae numerous, less than one half as long as primary setae; ventral elevations of abdominal sternum 9 usually with four distinct setae (occasionally three large and one smaller); pygopod bearing variable number of primary setae, 16–20 in second and third instars, 12–14 in first instar; median hooks of segment 5 with two to four setae (three in most individuals) in third instar, two setae in second instar, one seta in first instar; inner hooks with central spine approximately one third length of entire hook in third instar, one half of entire length in second instar, and two-thirds length of entire hook in first instar; two setae at shoulder of inner hook twice as long as spine (Figs. 30–32).

Measurements.— Third instar: Total body length, 12–20 mm (likely to vary greatly with nutritional state of individual and length of time since last moult); diameter of stemma I, 0.28–0.30 mm; diameter of stemma II, 0.25–0.29 mm;

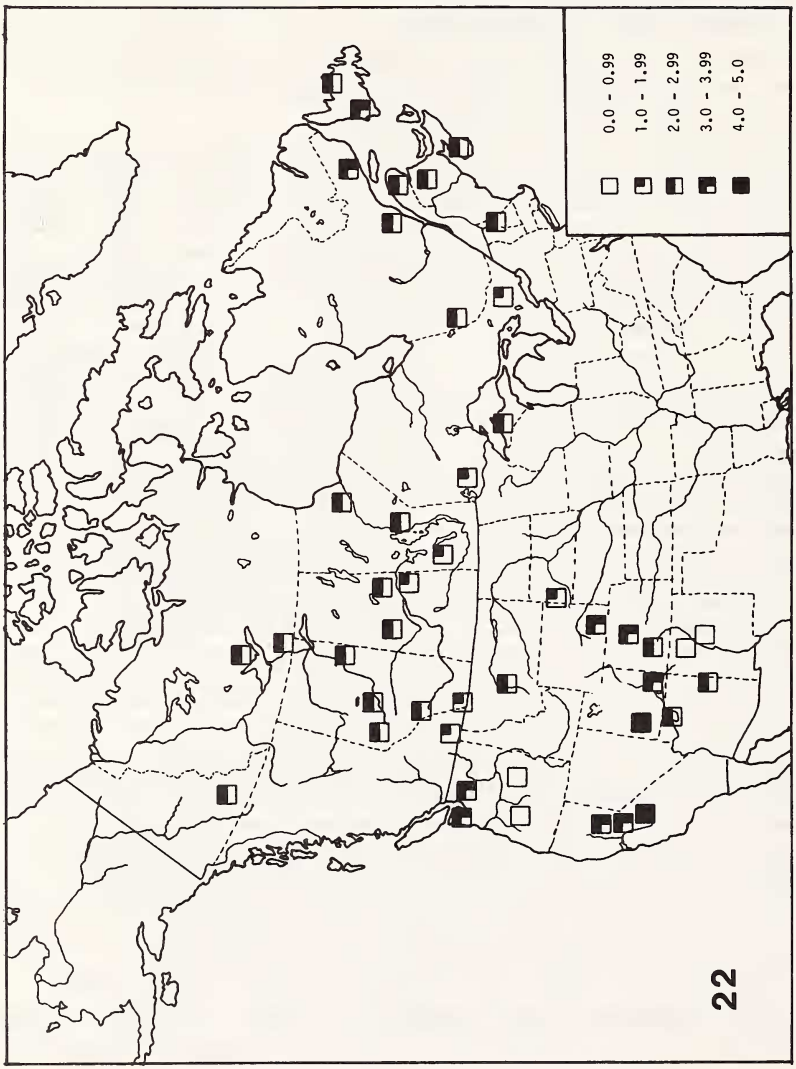


Fig. 22. Weighted mean character values of the humeral lunule (Fig. 8) of population samples of *C. longilabris* Say. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples are combined.

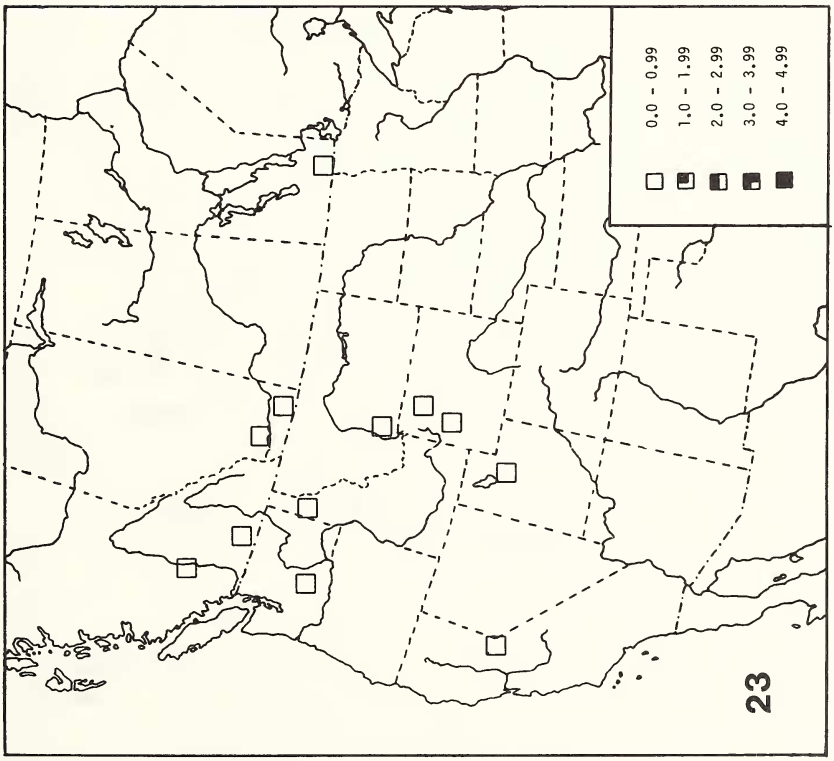


Fig. 23. Weighted mean character values of the humeral lunule (Fig. 8), for population samples of *C. nebraskana* Casey. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11.

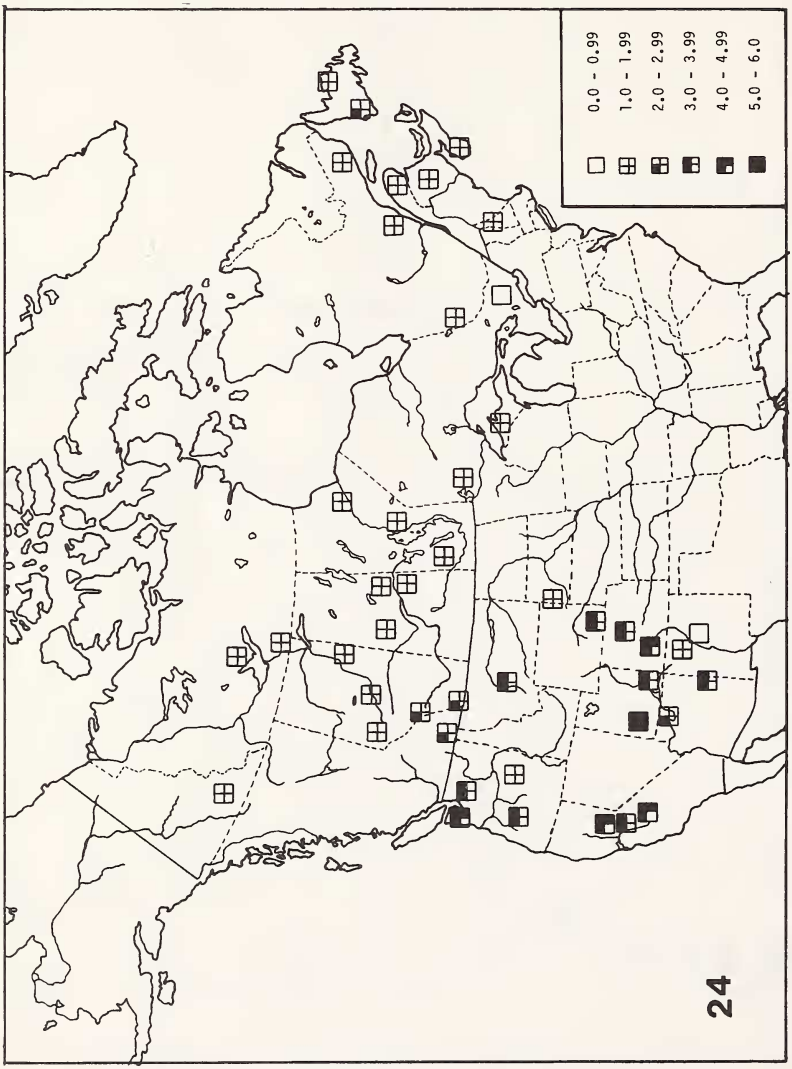


Fig. 24. Weighted mean character values of the middle band (Fig. 9) for population samples of *C. longilabris* Say. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11. The four Yukon populations samples are combined.

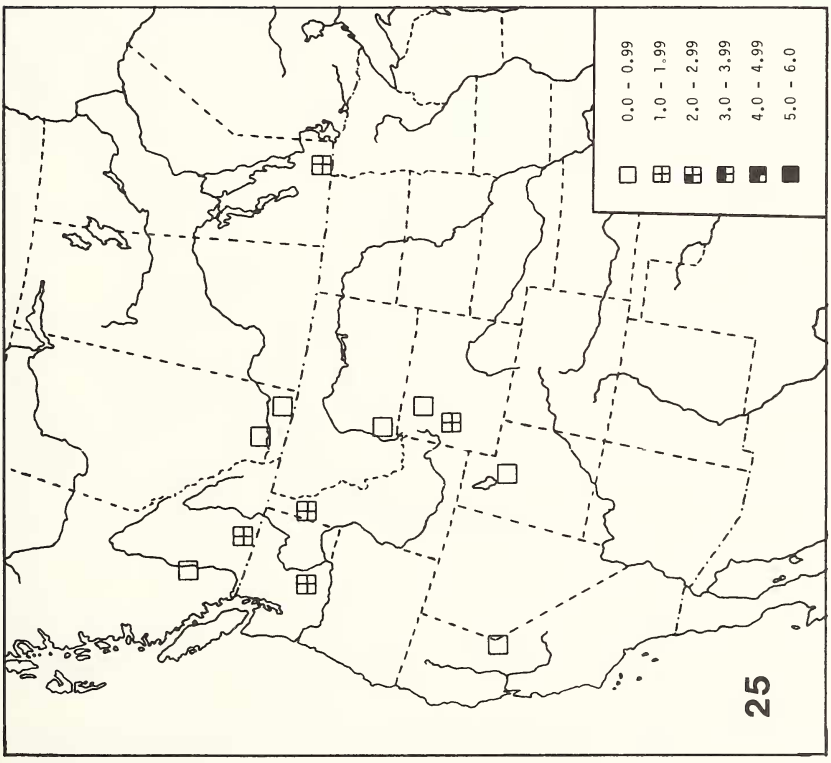


Fig. 25. Weighted mean character values for the middle band (Fig. 9), for population samples of *C. nebraskana* Casey. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11.

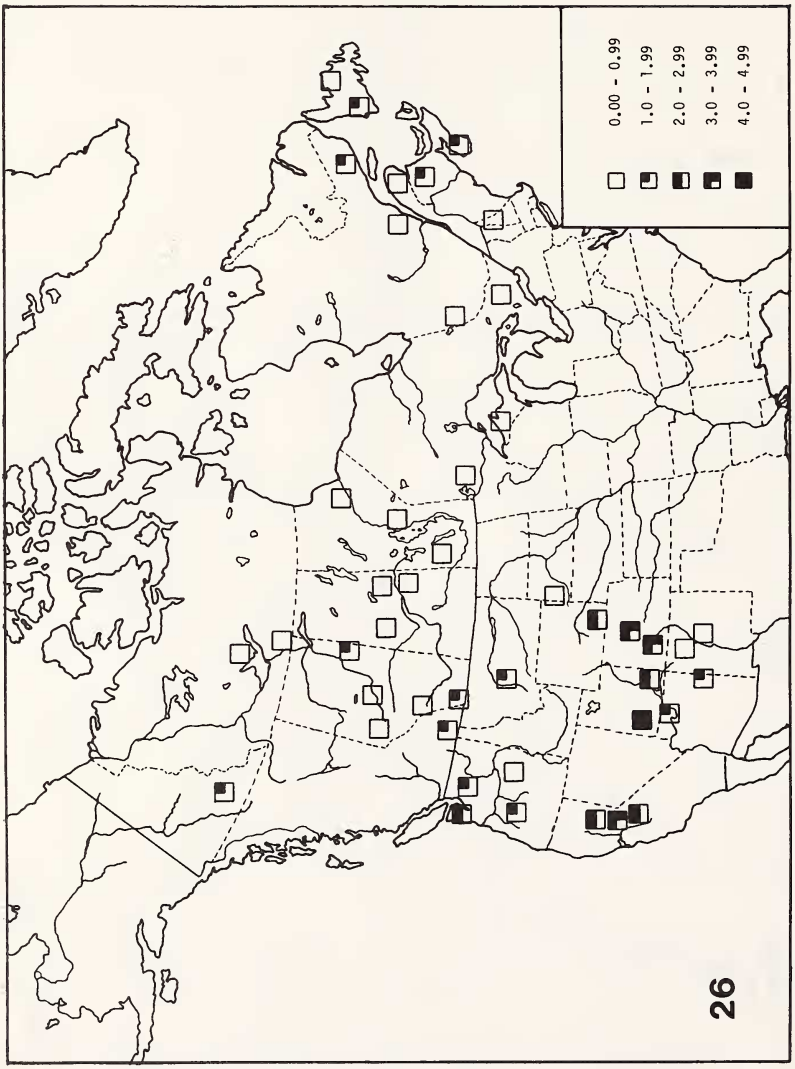


Fig. 26. Weighted mean character values of the apical lunule (Fig. 10), for population samples of *C. longilabris* Say. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11. The four studied Yukon population samples are combined.

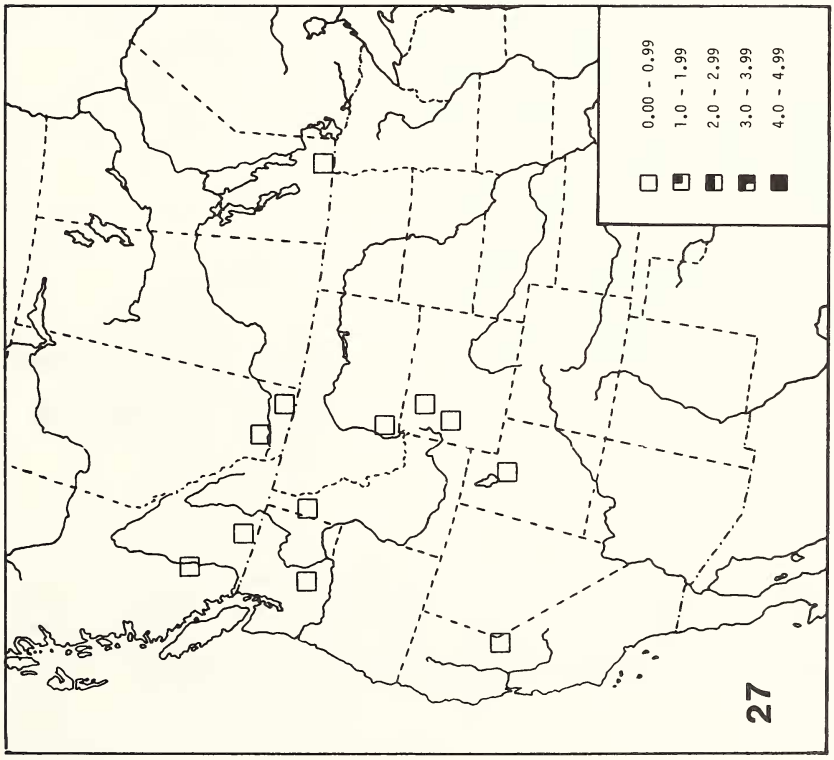
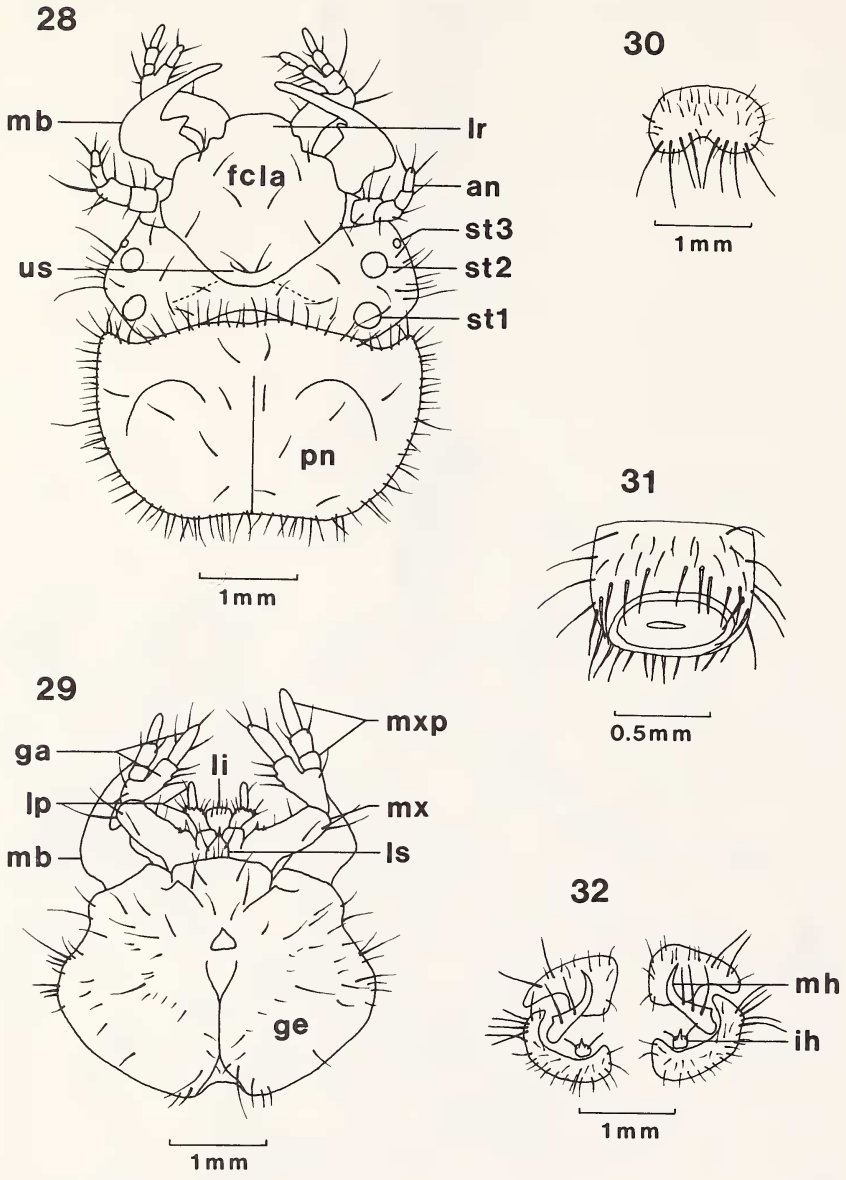


Fig. 27. Weighted mean character values of the apical lunule (Fig. 10), for population samples of *C. nebraskana* Casey. Data are summarized in Table 11. Population samples are indicated in Table 4 and Figure 11.



Figs. 28–32. Structures of the third instar larva of *C. longilabris longilabris* Say. 28, head and pronotum, dorsal aspect. 29, head, ventral aspect. 30, ninth abdominal sternum. 31, pygopod, dorsal aspect. 32, dorsum of fifth abdominal segment. Legend: an, antenna; fcla, frontoclypeolabral area; ga, galea; ge, genae; ih, inner hook; li, ligula; lp, labial palpus; lr, labrum; ls, labio-stipites; mb, mandible; mh, median hook; mx, maxilla; mxp, maxillary palpus; pn, pronotum; st1, stemma one; st2, stemma two; st3, stemma three.

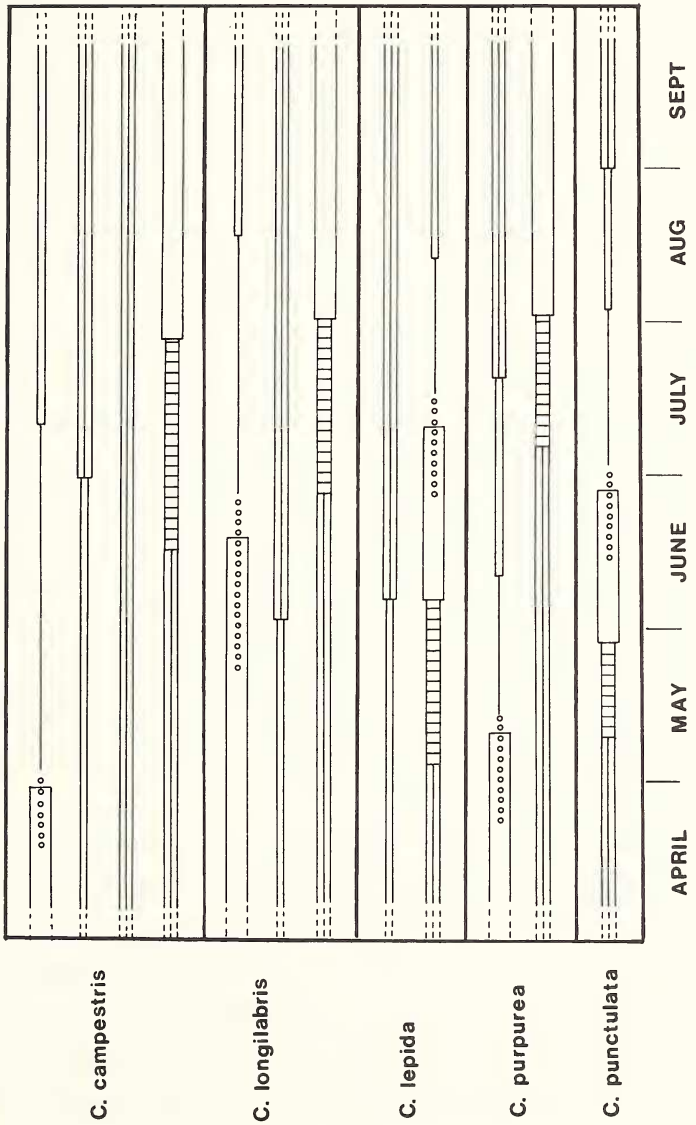


Fig. 33. Life cycle of *C. longilabris* Say compared with those of other species of *Cicindela* studied by Shelford (1908), and Huie (1915). The exact time of appearance and duration larval stages varies geographically and from year to year.

distance between stemma I and II, 0.26–0.33mm; length of frontoclypeolabral area 1.8–1.9 mm; length of pronotum, 2.00–2.22 mm; width of pronotum 3.44–3.61 mm. Second instar: Total length of body, 10–14 mm; length of pronotum, 1.26–1.40 mm; width of pronotum, 2.04–2.36 mm. First instar: Total length 4.7–7.1 mm; length of pronotum, 0.78–0.84 mm; width of pronotum 1.34–1.46 mm.

The three larval instars differ from each other in the following:

1 Size: The size of head and pronotum appears to occur in distinct size classes, as is evident for many other soil inhabiting tiger beetles in the work of Shelford (1908), Hamilton (1925), Willis (1967), Palmer (1978), Palmer and Gorrick (1979). The overall body size or abdominal size probably varies with nutritional state and the length of time the larva has had to grow since its most recent moult, which has been shown for *C. repanda* (Palmer and Gorrick, 1979), and for *C. japonica* (Hori, 1982).

2 Color of labrum: Because the metallic lustres are structural colors, they vary somewhat with the age of the individual as was shown by Shelford (1917). These colors also vary with different preserving fluids used.

3 Number of setae on the median hooks of the 5th abdominal segment differ between instars. First instars have one, 2nd instars have two, and most 3rd instars have three but number varies between two and four.

4 Number of setae on the mesal margin of galeomere 1 is one in 1st instars, two in 2nd instars, and three in 3rd instars, as noted by Leffler (1979).

5 Fewer setae are evident on each of the antennal segments in the earlier instars as indicated in the above descriptions.

A third instar larva of *C. longilabris* should run to couplet 18 in Hamilton's (1925) key, with a possible ambiguity at couplet 8 where variablility in number of setae on the median hook of abdominal segment 5 could cause uncertainty. As stated above, most 3rd instar larvae have three setae on the median hook, but some third and all earlier instar larvae have a smaller number. From couplet 18 of Hamilton's key, the larvae of *C. longilabris* can be separated from those of *C. tranquebarica* and *C. silvicola* by the following couplets:

1		Pronotal surface with numerous (less than 25) small secondary setae in addition to primary setae ..... *C. tranquebarica*
1'		Pronotal surface with one or two secondary setae 2
2	(1')	Pronotal surface with two setae on each side in addition to the six primary setae; distance between stemmata I and II greater than diameter of stemma II; Palearctic Region ..... *C. silvicola*
2'		Pronotal surface with one seta on each half in addition to the six primary setae; distance between stemmata I and II approximately equal to diameter of stemmata I and II; Nearctic

Region ..... *C. longilabris*

Life history.— In studying *Cicindela* species in the vicinity of Chicago, Shelford (1908) identified three life cycle patterns (Fig. 33). In a one year cycle such as that of *C. punctulata*, eggs are laid in mid-summer and larvae emerge and attain third instar by fall, hibernate as third instars, pupate the following June, adults emerge in early July and quickly become sexually mature, mate, oviposit and die within two months. In a two year cycle such as that typical of *C. lepida*, the eggs are laid in mid-summer, attain second instar by fall, hibernate as second instars, moult to third instars the second summer, hibernate a second winter as third instars, pupate the following spring, adults emerge early in the third summer, quickly become sexually mature, mate and die in two or three months. In an alternate two year pattern, such as that of *C. purpurea*, the eggs are laid in June, larvae attain third stage by fall, hibernate the first winter and pupate the following summer. Adults emerge late in the second summer, hibernate the second winter, emerge the next spring, mate, and die. In this last pattern larval life lasts approximately 13 months, and the adult stage lasts 12 to 13 months.

Shelford (1908) indicated that temperature, moisture, and food influence the duration of the larval stadia . Some of the species, which Shelford had found to have a two year cycle, as in the third pattern mentioned above, were found by Criddle (1910) to have a three year cycle farther north in Manitoba, where the larval life was prolonged over another winter. This is probably caused by shorter summer seasons which limit total food intake and delay progress through the larval stages. The work of Palmer and Gorrick (1979) and Hori (1982) indicates that the larvae of tiger beetles must attain a threshold body mass in each instar before moulting to the next stage can occur.

No studies of the chronology of *C. longilabris* or *C. nebraskana* through their immature stages have been published and information regarding adult seasonality of these species is limited. Leffler's (1979) observations of the unworn appearance of the elytra of adult *C. longilabris perviridis* collected in late summer, suggest that the adults emerge late in summer, overwinter and become sexually mature the following spring and, based on adult specimens collected in September which appeared teneral, he notes the same pattern of adult seasonality for *C. nebraskana*. Dunn (1978) provided a frequency histogram of *C. longilabris* specimens captured in New Hampshire which showed that adults were most frequently collected during the month of August. My data concerning the adult seasonality of these two species is consistent with the findings of Dunn (1978) and Leffler (1979).

Figure 34 indicates the total number of adult *C. longilabris* taken in each capture session at the Stanley Hill study site in 1982. Absolute population size was not estimated, but relative abundance at different times of the season was observed. June 5, 15, and September 2 were cool, overcast and rainy days when few beetles were active. The overall curve is bimodal. The number of specimens captured in the

August 24 session does not adequately represent the abundance of *C. longilabris* on that date. The technique used to mark and record the location and date of capture of each individual required a handling time which limited the total number of specimens which could be processed in one capture session. Specimens were so numerous on that day, that with each step eight or 10 adult specimens of *C. longilabris* could be seen to fly in many directions, and a few times two or three specimens were captured in one drop of the net. At other times of the season when beetles were not so numerous the upper limit on the number of individuals which could be captured, marked, recorded, and released was not approached.

Seventy-six per cent of the individuals captured on August 10 were teneral, 59 per cent of those captured on August 17th were teneral, and 66 per cent of those captured on August 24th were teneral, suggesting that the majority of specimens collected at that time of year had recently emerged from their pupae. The fact that very few of the specimens collected in May appeared teneral supports the hypothesis that most adults of this species emerge in late summer and overwinter in the imago stage.

The sex ratio of males to females of all adults of *C. longilabris* captured in May 1982 was 1.74:1 (n = 85). In June this ratio was 1.22:1 (n = 60), in July 1.57:1 (n = 18), in August 1.17:1 (n = 117) and in September 0.81:1 (n = 38). Freitag (1965) in examining seasonal changes in sex ratios of *C. oregona* and *C. decimguttata* found that females outnumbered males early in the season with males more numerous than females late in the season. The above data suggest that the reverse is true in *C. longilabris*. However, these ratios may not be indicative of the actual sex ratio in the population at any point in time. Kaulbars (1982) indicated that males of *C. denikei* were more numerous in prime open foraging areas of his study sites during breeding season, and at any given time a percentage of females were ovipositing in sites outside of foraging areas. As most of the oviposition occurs in early summer in *C. longilabris*, the apparent sex ratios skewed in favour of males at that time of year, could also be an artifact of such behavioural differences between the genders.

Few mating pairs of adult *C. longilabris* were observed at the Stanley Hill site during June and July. No mating pairs were seen after July 19th or any time during August or September. This is consistent with the hypothesis that adults emerging in late summer do not mate until the following spring.

Figure 35 illustrates frequency of capture of adult specimens of *C. longilabris* by date of collection from the label data of borrowed specimens collected in Canada. A bimodal pattern is weakly evident with population peaks in June and late August. There is probably a bias in these figures because insect collectors are usually more active during the summer months, in temperate climates. This may account for the relatively large numbers indicated for the month of July at a time of year when the relative abundance of *C. longilabris* was seen to decline at the Stanley Hill site (Fig. 34).

Figure 36 illustrates frequency of capture of adult *C. longilabris* from label data of borrowed specimens collected in the Pacific region states of Washington, Oregon and California and suggests a bimodal pattern of adult seasonal abundance. The large peak in the first half of July probably reflects the time of year when collectors are most active, and the second peak in September, at a time of year when collecting activity is greatly reduced, is probably indicative of a late summer emergence of adults from the pupal stage. Figure 37 presents the same type of histogram based on specimens from Utah, Colorado, Arizona and New Mexico. A bimodal frequency distribution is presented with greatest numbers occurring in early August. The pattern of seasonality of adults of *C. longilabris* is similar throughout its range, with some differences in the timing of late season emergence. In Canada the late season peak in numbers occurs in the latter half of August (Figs. 34, 35), in the southern Rocky Mountain region this seems to occur in the early half of August (Fig. 37), and in the Pacific coast states in early September (Fig. 36).

Figure 38 presents the frequency of capture of *C. nebraskana* adults by date from label data of pinned specimens. This species appears to be less abundant during mid-summer and experiences a population peak in late summer. Thus *C. nebraskana* probably has a life cycle in which adults emerge in late summer and overwinter before mating the following spring and early summer. This hypothesis, of course, awaits confirmation from field studies of the species.

The marking of larval burrows and subsequent observations of development in size and condition of the burrows at the Stanley Hill site in the summer of 1982 yielded three patterns of seasonality.

Third instar burrows marked in May and early June all disappeared after approximately mid June. Specimens either died, had their burrows disturbed, or closed their burrows, pupated and later emerged as adults. In some instances the burrows and golf tees marking them were disturbed by off-road motorcycles and lawn mowers.

Seven third instar larvae dug from burrows and placed in rearing tubes in May pupated in June and emerged as adults of *C. longilabris* in late July. These burrows were closed between the active 3rd instar stage and emergence of the adult for an average of 46 days, ranging from 39 to 62 days. The specimens were probably not in the pupal stage all of that time. Actual duration of the pupal stage is not known as it was not observed directly.

The majority of specimens marked as 2nd instars at the Stanley Hill site in May and June were not successfully followed through the season, presumably from mortality. Those followed through the season were found to have attained 3rd instar by early June. They continued to feed for most of the summer and were still in the third instar in the third week of September. They presumably would have overwintered in this stage.

First instar larvae appeared on the second week of July and were found in increasingly large numbers throughout July. The majority were not followed

through the duration of the summer, probably because of a high mortality rate. Those which were successfully followed through the summer had attained the 2nd instar by the first or second week of September and presumably overwintered in the 2nd stage.

One first instar larva found in early May at the Stanley Hill site had probably overwintered. It was probably an individual which had not acquired sufficient body mass to moult to 2nd instar before its first winter. Such variant individuals are to be expected.

These data indicate that the complete life cycle of *C. longilabris* is three years in duration. Figure 33 presents the chronology of the three year cycle of *C. longilabris* compared with the cycles of other species studied by previous workers (Shelford, 1908; Huie, 1915).

If the chronology of the life cycle were rigid for all individuals, *C. longilabris* would consist of three distinct populations each genetically and temporally isolated from the other two. Many workers (Shelford, 1908; Willis, 1967; Palmer, 1976) have indicated some variablility in timing of appearance of the life stages in many species of tiger beetles. Hori (1982), in studying *C. japonica* in which the seasonality of the adult stage is similar to that of *C. longilabris*, indicated that few adults emerging late in summer achieve sexual maturity quickly and a small amount of oviposition occurs in late summer and early fall. An intensive study of the population dynamics of *C. longilabris* would probably reveal a similar amount of variability in the timing of life stages. Slow developing larvae as mentioned above, and a small amount of late season mating would maintain a genetic connection between year classes.

It is unlikely that the life cycle of *C. longilabris* is less than three years in duration anywhere in the geographical range of the species. Even in the southern part of its range in Arizona, New Mexico and Colorado, the same pattern of adult seasonality seems to occur (Fig. 37). In such areas these beetles inhabit montane and subalpine forests at high elevations where the duration and temperature ranges of the seasons roughly approximate that of the boreal forest zone father north. Possibly the cycle may take a year longer in the more northern part of its range. Just as some species of *Cicindela* which have two year cycles in the Chicago vicinity (Shelford, 1908) were found to have three year cycles in Manitoba (Criddle, 1910), the larvae of *C. longilabris* may take an extra year to develop in the northern part of its range where it approaches tree line and the southern limit of continuous permafrost (Fig. 39), and where the summer season is appreciably shorter. This is, of course, speculative and field work would have to be carried out in various parts of the range of the species to test the hypothesis.

Soil Associations

Leffler (1979) contended that edaphic factors are among the most important limits in defining the habitats of ground-dwelling tiger beetles. The female chooses

TABLE 12. Frequency, and relative frequency (%), of occurrence of locality records of *C. longilabris* and *C. nebraskana* on dominant soil types as indicated by soil maps (see text for details).

	C. longilabris										*C. nebraskana*			
	Eastern North America		Prairie Provinces		North-western North America		Pacific States		Cordilleran States		Summary All Areas			Summary
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
Chernozem: Brown	-		-		-		25	(21)	3	(1.5)				
Dark Brown	-		2	(2.6)	-		2	(1.7)	1	(0.5)	97	(12.8)	105	(34.1)
Black	-		19	(25)	-		-		35	(17.3)			72	(23.4)
Dark Gray	-		4	(5.3)	-		-		6	(3)			32	(10.4)
													6	(1.9)
Solonetz	-		-		-		-		2	(0.3)	2	(0.3)	5	(1.6)
Solod	-		1	(1.3)	-		-		-		1	(0.1)	-	
Luvisol: Gray Brown	-		-		-		7	(6)	7	(3.5)			5	(1.6)
Gray	33	(11)	19	(25)	5	(12)	46	(39)	100	(49.5)	217	(28.6)	18	(5.8)
Podzol: Humo-Ferric	233	(75)	4	(5.3)	9	(21)	-		-		246	(32.5)	2	(3.2)
Brunisol: Melanic	12	(3.8)	-		-		-		9	(4.5)			-	
Eutric	-		1	(1.3)	15	(36)	34	(29)	23	(11.4)	103	(13.6)	17	(5.5)
Distric	9	(2.9)	-		-		-		-				9	(2.9)
Regosol	13	(4.1)	-		-		-		6	(3)	19	(2.5)	16	(5.2)
Rockland	1	(0.3)	10	(13.2)	5	(12)	-		-		16	(2.1)	-	
Gleysol	6	(1.9)	-		4	(9.5)	-		-		10	(1.4)	3	(1)
Fibrisol & Mesisol	5	(1.6)	13	(17)	-		-		-		18	(2.4)	-	
Borderline Cases	9	(2.8)	3	(3.9)	4	(9.5)	4	(3.4)	10	(5)	30	(4)	18	(5.8)
Total (N)	312	(100)	76	(100)	42	(100)	118	(100)	202	(100)	759	(100)	308	(100)

Summary N	(%)
215	(70)
5	(1.6)
-	
23	(7.4)
2	(3.2)
26	(8.4)
16	(5.2)
-	
3	(1)
-	
18	(5.8)
308	(100)

TABLE 13. Characters and character states classified phylogenetically, and their distribution among the species of the *C. sylvatica* group.

No.	Character	Species and character states							
		nebr.	long.	sylv.	gran.	jap.	gemm.	solu.	lact.
17	Female gen.: quadrate sclerite	0	0	0	0	1	0	0	0
16	Female gen.: oviduct sclerite	0	0	0	0	A	B	0	0
15	Female gen.: second gonapophyses	0	0	0	0	0	1	1	0
14	Antennal scape: 'other setae'	0	0	A	A	0	0	B	0
13	Labrum: color	1	1	1	0	0	0	0	0
12	Size	1	1	1	1	1	1	0	0
11	Labrum: median longitudinal ridge	A1	A1	A2	A1	A1	A1	A1	0
10	Labrum: length/width	1	1	1	1	0	0	0	1
09	Elytra: surface texture	A	0	0	0	0	0	B	B
08	Frons: setae	1	1	0	0	1	0	0	1
07	Elytra: color of dorsal surface	0	0	0	0	A	A	A	B
06	Apical lunule	A2	A1	A1	A1	A1	0	0	B
05	Middle band	A	0	0	0	0	0	0	B
04	Humeral lunule	A2	A1	0	A1	A1	A1	A1	B
03	Male gen.: sclerites of internal sac	0	0	0	0	A	B	B	C
02	Male gen.: apex of aedeagus	0	0	A	A	0	0	0	B
01	Female gen.: eighth sternum	0	0	0	A	A	0	B	C

0=plesiotypic character state; 1=apotypic character state; alphanumeric symbols indicate transformation series and modifications of characters (see text for details). The outgroup (the *Cicindela maritima* species group) exhibits the plesiotypic state for each character.

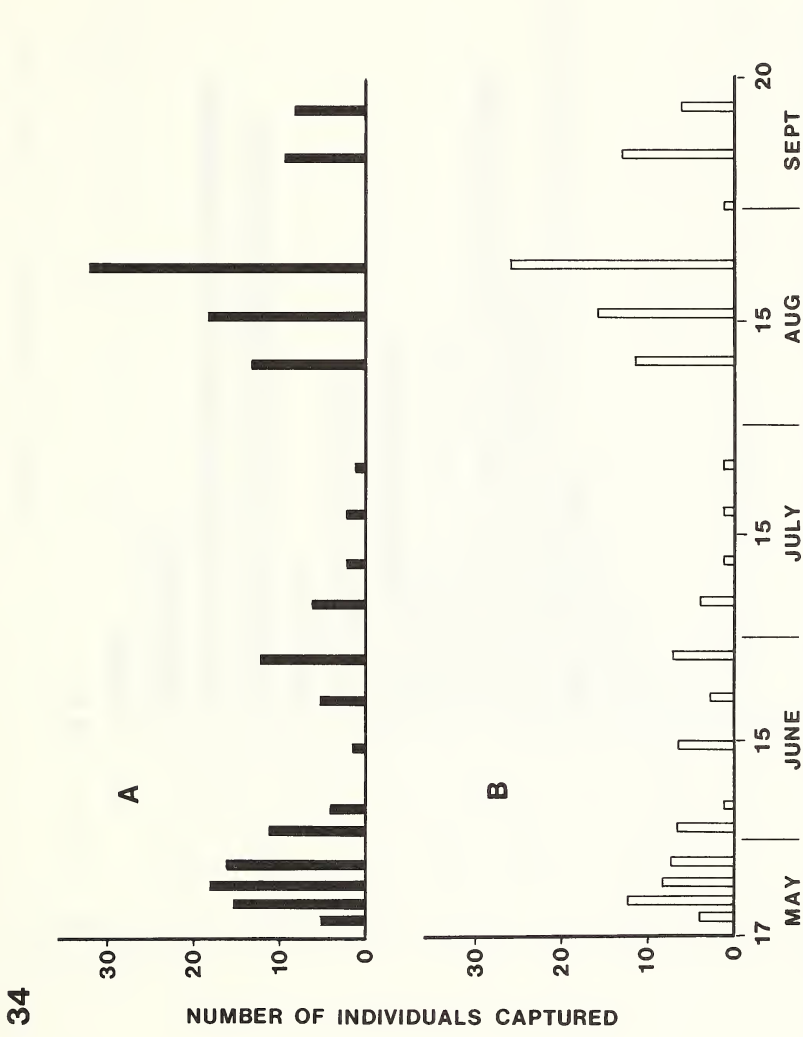


Fig. 34. Total catch of *Cicindela longilabris* Say, Stanley Hill study site, Thunder Bay District, Ontario, in the summer of 1982. A, males; B, females.

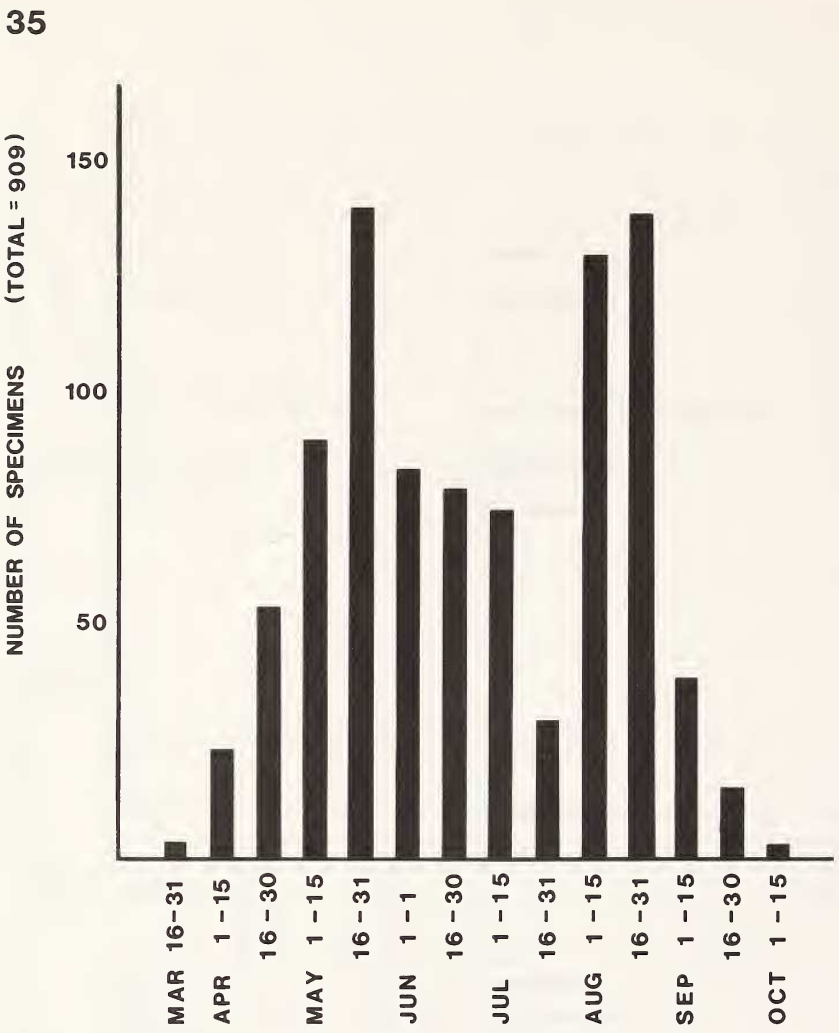


Fig. 35. Collection dates of borrowed adult specimens of *Cicindela longilabris* Say , collected in Canada.

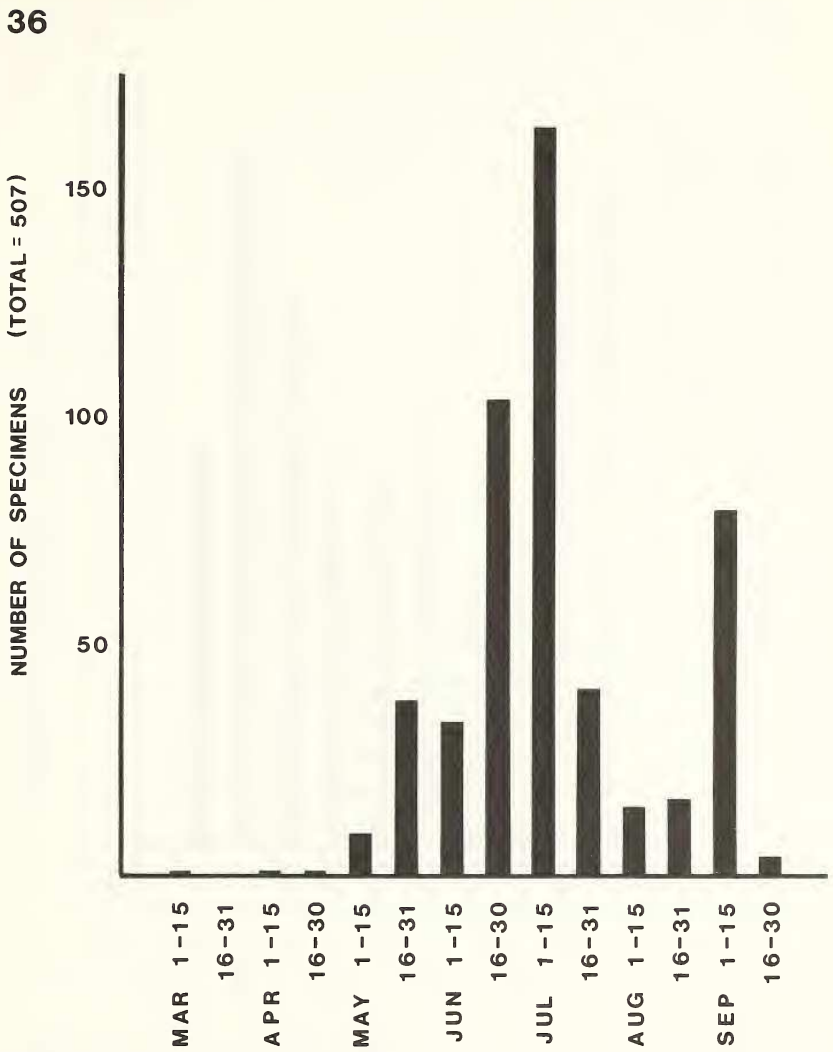


Fig. 36. Collection dates of borrowed adult specimens of *Cicindela longilabris* Say, collected in Washington, Oregon and California.

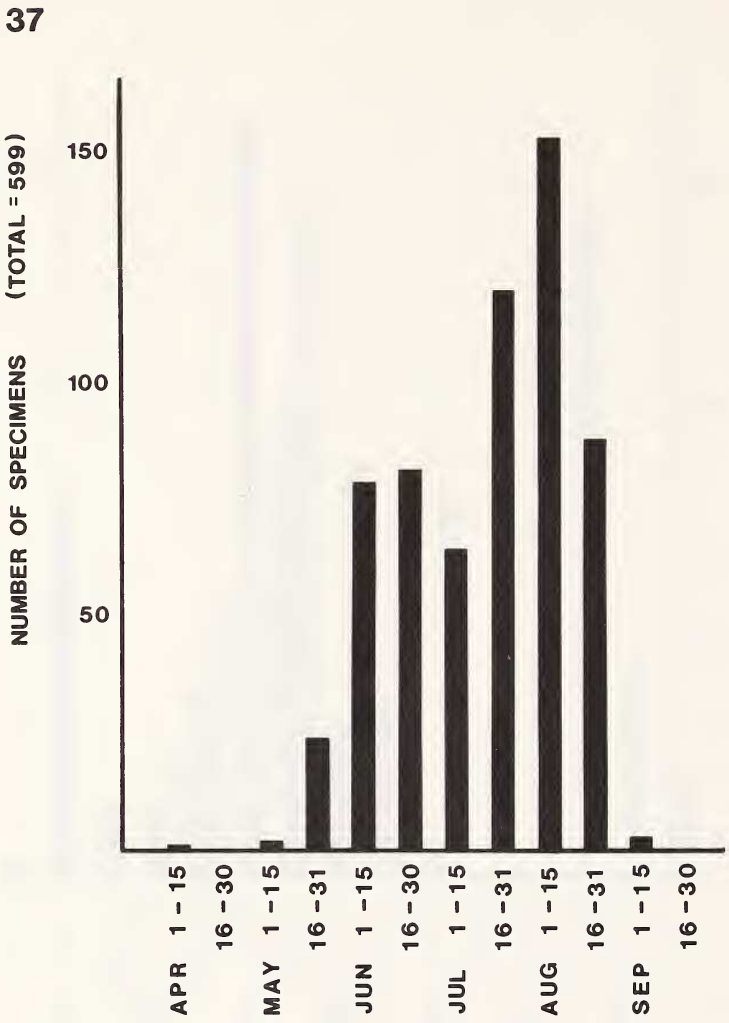


Fig. 37. Collection dates of borrowed adult specimens of *Cicindela longilabris* Say, collected in Colorado, Utah, Arizona and New Mexico.

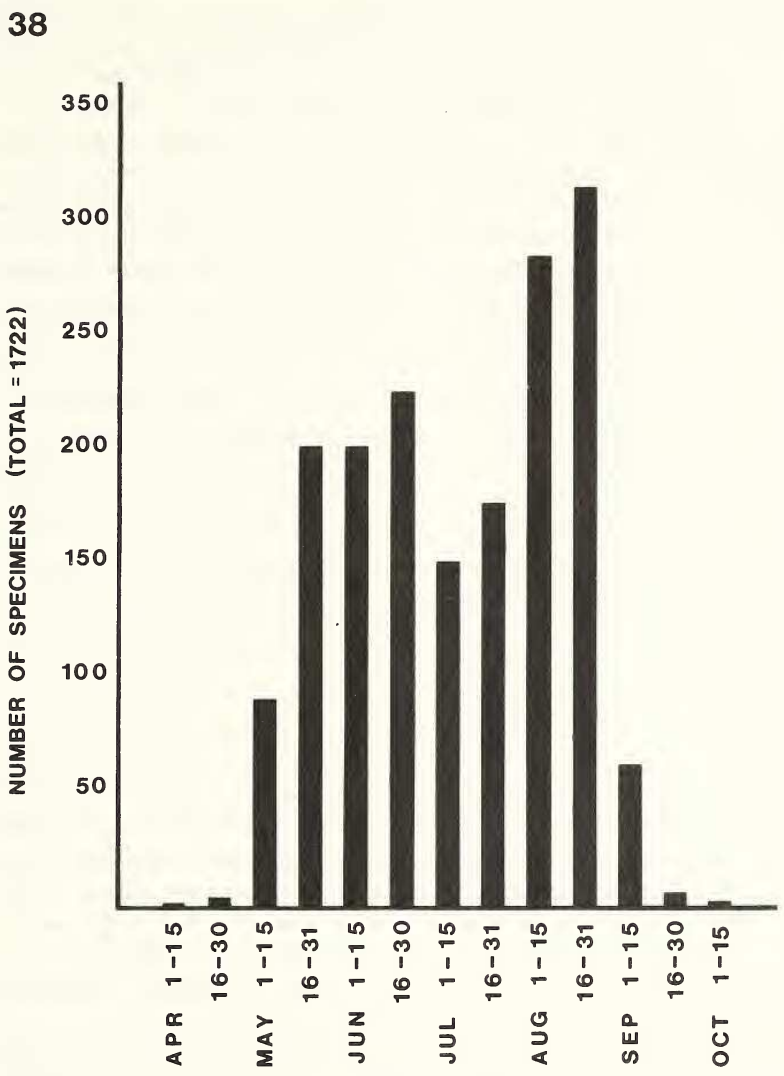


Fig. 38. Collection dates of borrowed adult specimens of *Cicindela nebraskana* Casey.

the oviposition site (Shelford, 1907) and the entire larval stage is spent in a burrow in the soil. Many species are restricted to soils of particular types such as clay, sand, or alkali-encrusted, among others. Kaulbars (1982) reported that soil type seemed to be a limiting factor in the distribution of some forms of the *C. sexguttata* species group. Leffler (1979) noted a correlation between the length of the second gonapophyses of the female genitalic armature used in oviposition and the particle size of soil inhabited, among 15 species of *Cicindela*. He concluded that species with long narrow styli are in soils with a high proportion of sand and those with short stout styli inhabit soils with a high clay content, adding a cautionary note that recently eclosed individuals should be examined in such a test, as digging activity can greatly wear down the length of the styli making them much shorter and more blunt in older individuals. Depending upon how this wearing of the second gonapophyses affects the sensory abilities of the female to detect differences in soil qualities such as texture, it raises the question of whether eggs laid by an older female might be laid in soil of a slightly different texture or at a different depth than those laid earlier in the life of a given female, and how these factors in turn might affect the survival chances of the eggs. If such differential survivorship occurs it could be a strong selective force favouring individuals laid at a certain stage in the life of an adult female, thus tending to stabilize a given life cycle pattern for a given species. Intensive field studies of oviposition site selection by females and subsequent larval survivorship would have to be undertaken to answer these questions.

Leffler (1979) also concluded that the mean ratio of breadth/length of the styli of the second gonapophyses is not statistically significantly different between *C. longilabris* ($\bar{X}$ = 56.75) and *C. nebraskana* ($\bar{X}$ = 56.95). According to Leffler's (1979) hypothesized relationship between the dimensions of the second gonapophyses and soil texture, one would not expect a significant difference in the distribution of particle size of the soils inhabited by these two species. Leffler (1979) however, indicated that there is such a difference. He stated that five samples of soil from collecting sites for *C. longilabris* are largely clay soils, with a mean of 28.6% sand, in contrast with five samples of soil from collecting sites for *C. nebraskana* which are all sandy clay with a mean of 50% sand.

My data are more consistent with Leffler's (1979) indicated similarities between the dimensions of the 2nd gonapophyses of these two species. Using 0.63 mm diameter as the border between sand and gravel (>0.63 mm dia.), and silt and clay (<0.63 mm dia.), samples taken from widely distributed collecting sites for *C. longilabris* averaged 82% sand and gravel and three samples from sites for *C. nebraskana* averaged 83% sand and gravel. In each sample gravel (particles >2.0 mm diameter) made up a very small fraction. Although the sample sizes are too small to be conclusive, these data suggest that both species occur on sandy soils in which silt and clay are minor components.

Edaphic factors other than particle size, such as pH, electroconductivity, moisture and temperature of soil, amount of organic matter present, and chemical make-up could be important in the distribution of the two species.

By plotting collecting localities from specimen label data on soil maps, comparisons were made between the distributions of the different forms of *C. longilabris* and *C. nebraskana* and those of the major dominant soil types at the order and great group level of classification. Table 12 shows the percentages, and absolute number of locality records occurring on dominant soil types for *C. longilabris* and *C. nebraskana*. Some general trends are apparent.

C. longilabris occurs predominantly on soil types which develop under the influence of forest vegetation. In eastern North America (from northern Ontario and Minnesota east) the great majority of locality records of *C. longilabris* are on map units indicating Humo-Ferric Podzols as the dominant soil type (Soil Conservation Service, 1967; Soils of Canada, 1972). Soils of the podzolic order, in the Canadian classification are well to imperfectly drained mineral soils which typically develop under coniferous or mixed forest or heath vegetation and characteristically have complexes of soluble organic matter and compounds of aluminum and iron leached from the surface layers and deposited in the B or subsurface horizon (Clayton *et al.*, 1977). The Humo-Ferric great group is widely distributed in Canada, being the dominant soil type in all podzolic map units indicated on the Soils of Canada (1972) map. Humo-Ferric Podzols occur mainly on well drained sites and are characterized by B horizons in which accumulations of aluminum and iron colloids are considered most significant to their properties, and the organic matter content of the B horizon is less than 10% (Clayton *et al.*, 1977).

In the prairie provinces a number of soil types are indicated, with Gray Luvisols (25%) and Black Chernozems (25%) accounting for the greatest percentage of the locality data for *C. longilabris* (Table 12). Gray Luvisols are well to imperfectly drained mineral soils that have developed under the influence of the decomposition of forest vegetation in mild to cold climates and have silicate clays as the major accumulation product in the B or subsurface horizon (Clayton *et al.*, 1977). Black Chernozems are typical of the Aspen Parkland or Fescue Prairie transition zone between the treeless grasslands of the Mixed Prairie, and the true Boreal Forest (Clayton *et al.*, 1977).

In the northwestern part of the continent (Alaska, Northwest Territories, Yukon, and British Columbia), most localities seem to be on Eutric Brunisols and Humo-Ferrric Podzols. Brunisols are defined by Clayton *et al.* (1977) as a broad grouping of imperfectly to well drained soils which have developed under the influence of forest, alpine, or tundra vegetation, under climatic conditions varying from Mesic to Arctic, and widely varying moisture regimes, in which the processes of leaching and weathering are weakly developed, so they tend to reflect the chemical characteristics of the parent material. Eutric Brunisols are base saturated soils developed under forest or alpine vegetation, and usually occur on basic or

calcareous parent materials.

In the Rocky Mountain states (which for the sake of this discussion include Idaho, Montana, Wyoming, the Black Hills area of South Dakota, Colorado, Arizona, New Mexico, and parts of Nevada and Utah) *C. longilabris* appears to occur primarily on montane, or Canadian Zone forest on associations of dominantly Luvisolic and subdominant Podzolic soils (Table 12). In the Pacific Coast States most of the localities seem to occur on associations of Luvisols and Brunisols (Table 12).

Soil associations of *Cicindela nebraskana* are notably different from *C. longilabris*. Most collecting records of *C. nebraskana* were on map units where Chernozemic soils are dominant (Table 12). In the Canadian classification (Clayton *et al.*, 1977) Chernozemic soils are well to imperfectly drained soils of good structure with dark colored virgin or cultivated A horizons, overlying subsurface horizons of high base saturation. These soils develop within areas of cool to cold continental climates, their humus enriched A horizons are developed and maintained by cyclic growth and decay of xerophytic to mesophytic grasses and forbs typical of grasslands and grassland-forest transition communities. They are typical of the Canadian prairies and rangelands of interior British Columbia (Clayton *et al.*, 1977), which are the areas in Canada where *C. nebraskana* occurs.

In summary, throughout most of the ranges of *C. longilabris* and *C. nebraskana* a separation between species is apparent at the level of soil orders. The former occurs almost exclusively in areas of Podzolic soils in the eastern half of this continent, and on Luvisols, Brunisols and Podzols, soils of montane and subalpine forest and alpine and arctic meadows in the west. In contrast, *C. nebraskana* occurs primarily on Chernozemic soils of grasslands and grassland-forest transition zones. Across the Canadian prairies the ranges of the two species are sympatric in a broad zone occurring in the area where Black Chernozems predominate (see maps in Clayton *et al.*, 1977), which approximates the Aspen-Oak and Aspen Grove transition zone between prairie grassland and Boreal forest (Rowe, 1972).

More field study of these species is required to elucidate the nature of the ecological separation which seems apparent from the above comparisons of beetle distributions and soil maps. For example, in the above mentioned Aspen Grove regions of Alberta and Saskatchewan more intensive study in the field would likely show that the two species, though sympatric in a coarse geographic sense, are separate on a local scale, and exhibit different soil preferences. Similarly in some areas of the Pacific States and southern British Columbia adults of the two species have been collected at the same sites (Leffler and Pearson, 1976; Norman Rumpp, pers. comm.). Additional field study may show that these are merely points of local parapatry. Leffler and Pearson (1976) have indicated that the form they referred to as *C. longilabris ostenta* occurs in the Hudsonian and Alpine-Arctic life zones of the Olympic Peninsula and Cascade Mountains in Washington State, whereas *C. nebraskana* approximately follows the distribution of the Ponderosa

Pine-Bunchgrass vegetation association in that state.

CLASSIFICATION OF THE NEARCTIC TAXA OF THE *CICINDELA SYLVATICA* GROUP

Cicindela longilabris Say

Cicindela longilabris longilabris Say 1824:268. **Neotype, New designation (MCZ).** Type locality: Silver Islet, Sibley Prov. Pk., Ontario, here designated. LeConte, 1848:178. 1860:33. 1861:338. Leng, 1902:119. Harris, 1911:20. Horn, 1915:377. 1928:11. 1930:82. Rivalier, 1954:252. Lindroth, 1955:19. 1963:93. Wallis, 1961:46. Graves, 1963:501. 1965:67. Leffler, 1979:467. Boyd and Associates, 1982:6.
Cicindela albilabris Kirby, 1837:12. Type locality: "Taken in Lat. 64 degrees and also in Canada...". Emmons, 1854:36.
Cicindela longilabris albilabris; LeConte, 1848:178. 1860:33. Casey, 1913:17.
Cicindela longilabris novaterrae Leng, 1918:141. Type locality: Bay St. George, Newfoundland. Wallis, 1961:46. Boyd and Associates, 1982:6. **New Synonymy.**
Cicindela oslari terracensis Casey, 1924:13. Type locality: Terrace, British Columbia.
Cicindela var. *nebraskana*; Horn, 1928:11.

Cicindela longilabris laurentii Schaupp, 1884:87. Type locality: Colorado. Leng, 1902:121. Harris, 1911:20. Casey, 1913:20. Leffler, 1979:474. Boyd and Associates, 1982:6.
Cicindela longilabris oslari Leng, 1902:121. Type locality: San Francisco, San Miguel Mountains, Colorado. Harris, 1911:20. Boyd and Associates, 1982:6. **New Synonymy.**
Cicindela longilabris vestalia Leng, 1902:121. Type locality: Maiden, Montana.
Cicindela oslari densissima Casey, 1924:12. Locality unrecorded, "probably Colorado".
Cicindela oslari estesiana Casey 1924:13. Type locality: Colorado.
Cicindela laurenti; Casey, 1924:13. Tanner, 1929:82. Dahl, 1941:189.
Cicindela montana laurenti; Wallis, 1961:plate 3.

Cicindela longilabris perviridis Schaupp, 1884:87. Type locality: Sierra and Placer Counties, California (restricted by Leng, 1902). Harris, 1911:20. Horn, 1915:377. 1930:82. Leffler, 1979:477. Boyd and Associates, 1982:6.
Cicindela perviridis; Leng, 1902:122.
Cicindela ostenta Casey, 1913:17. Type locality:California.
Cicindela perviridis placerensis Casey, 1913:18. Type locality: Placer Co., California.
Cicindela ostenta columbiana Casey, 1924:13. Type locality: British Columbia.
Cicindela montana perviridis; Wallis, 1961:50.
Cicindela longilabris ostenta Leffler and Pearson, 1976:29. Boyd and Associates, 1982:6. **New Synonymy.**

Cicindela longilabris laurentii X Cicindela longilabris perviridis
Cicindela montana oslari; Wallis, 1961:50.
Cicindela montana laurenti; Wallis, 1961:50.
Cicindela longilabris oslari; Leffler and Pearson, 1976:29.

Recognition.— The convex and elongate labrum, bald, broadly excavated head and non-serrate elytral apices are sufficient to distinguish adult specimens of *C. longilabris* and *C. nebraskana* from those of all other North American species of *Cicindela.*

Adults of *C. longilabris* are distinguished from those of *C. nebraskana* by the more coarse, frequently confluent, granulate punctations on the elytral surface, usually metallic green abdomen, at least in part, or a combination of metallic green, green and blue, or green and bronze, and by a pattern of maculations on the elytra including, in most specimens, a humeral and/or post humeral spot or complete

lunule, a sloping, elbowed middle band, and an apical lunule varying from an apical spot to an entire lunule.

Notes about synonymy and taxonomic history.— There has been much confusion between *C. longilabris* and *C. nebraskana* because of the similarities between individuals of the latter species and less maculate specimens of the nominate form of *C. longilabris*. The fact that populations of the two species can in some places be found in the same locality where their habitats are immediately adjacent, increases the confusion.

I have shown evidence from discriminant analysis, statistical differences in size and proportion of labrum and ratio of head width to pronotal width, differences in qualitative characters such as female labrum color, color of ventral abdominal surface, elytral surface and proepisternum, differences in patterns and extent of markings, as well as an apparent ecological separation based on differences in distribution relative to major soil types, why two species should be recognized. This view is supported by the observations of Rumpp (pers. comm.) and Leffler and Pearson (1976), that no apparent hybridization occurs where sympatric populations of *C. longilabris perviridis* and *C. nebraskana* occur in California and Washington State.

Kirby's (1837) description of *C. albilabris* is sufficient to establish its identity as the same as Say's (1824) *C. longilabris*. Lindroth (1953) examined Kirby's type specimen in the British Museum (Natural History), a male from Nova Scotia, and concluded that it was the same as the nominate form of *C. l. longilabris*.

Green specimens from the island of Newfoundland were given the subspecific name *C. l. novaterrae* by Leng (1902). I believe that, because of the discordant pattern of variation between Newfoundland and mainland samples shown by the discriminant analyses (Tests 1 and 2, Tables 5, 6 and 7), and the fact that large numbers of brown and black specimens are on the eastern part of the island (Lindroth, 1963), and green specimens can be found on the mainland of Québec and Labrador, the formal naming of the Newfoundland populations is inappropriate.

A single specimen from Terrace, British Columbia, which Casey (1924) described as *C. oslari terracensis* is black, with the body size, ventral coloration and elytral markings typical of *C. longilabris longilabris* Say.

Horn (1928) incorrectly applied the name *Cicindela* var. *nebraskana* to specimens of *C. longilabris* from Minnesota, which exhibited reduced maculation.

The name *C. l. laurentii* has historically been applied to olive green, heavily maculate specimens from the Rocky Mountain region of the United States, and the name *C. l. oslari* has been applied to specimens from the same region, which exhibit less extensive maculation and dorsal coloration varying from green to bronze to brown.

Leng (1902) described *C. l. vestalia* based on immaculate specimens from Maiden, Montana which are, in all other characters, within the range of variation found in *C. l. laurentii* throughout the Rocky Mountain region of the United States.

Specimens described by Casey (1924) as *C. oslari densissima* and *C. oslari estesiana* from Colorado were based on slight individual variations in coloration and maculation which are within the range of variation to be found in populations of *C. l. laurentii* in Colorado.

Wallis (1961) confused the relationships between the forms in this group, classifying *C. m. laurentii* (*sic*), *C. m. oslari* and *C. m. perviridis* as subspecies under the species name *C. montana*. Wallis applied the names *C. montana oslari* and *C. montana laurenti* (sic) to populations in south central British Columbia which are in a hybrid zone where the Pacific Coast, Rocky Mountain and boreal forms of *C. longilabris* converge and produce populations with a high degree of individual variation. Specimens from eastern Washington state referred to as *C. longilabris oslari* by Leffler and Pearson (1976) are also from the area of hybridization of the Pacific coast, Rocky Mountain and boreal forms of *C. longilabris*

Schaupp (1884) originally described *C. l. perviridis* as occurring in California, Oregon, Utah and Newfoundland. Leng (1902) narrowed the type area of this form to Sierra and Placer counties in California, distinguishing *C. l. perviridis* from any Rocky Mountain or Boreal forms which also exhibit a green coloration.

Notes on designation of a neotype for C. longilabris Say.— Thomas Say's private collection was entirely destroyed after his death (LeConte, 1859 p. vi). It would seem to be in the interest of stability of nomenclature, in light of the confusion which has occurred in the identification and interpretation of the species *C. longilabris* and *C. nebraskana* to designate a type specimen for the former. Lindroth and Freitag (1969) expressed the desirability of designating neotypes to stabilize Thomas Say's names, and Leffler (1979) and Huber (pers. comm.) have opined that a neotype should be designated for *C. longilabris*.

Say had distributed specimens from his collection to Dejean in France (Lindroth and Freitag, 1969). Dejean (1826) indicated that he had received specimens from Say and he redescribed many of Say's species (Dejean, 1825–1831). However, *C. longilabris* was not among them. Dejean (1837) did not list *C. longilabris* in the catalogue of his collection. It appears that none of Say's specimens of *C. longilabris* exist from which to choose a type.

Say (1824) indicated nothing more exact than "Northwest Territory" for a type locality. Wallis (1961) indicated the approximate route of the second expedition of Major Long to the source of the St. Peter's River in 1823, the trip on which Thomas Say would have collected this species. It started in Philadelphia, from where the party travelled to Chicago, Minneapolis, and to Big Stone Lake on the border between Minnesota and the northeast corner of South Dakota. From there the route led down the St. Peter's River (now called the Red River) to Lake Winnipeg, and from there east to Lake of the Woods, around the north shore of Lake Superior and southward toward Lake Ontario. Wallis (1961) correctly points out that *C. nebraskana* does not occur throughout most of the route, but *C. longilabris* could be

collected anywhere from the Lake Winnipeg area, past the north shore of Lake Superior and southward much of the way toward Lake Ontario.

LeConte (1859) was very familiar with the work of Say, and was probably referring to Say's material when he redescribed *C. longilabris* (1860). LeConte's redescription, though in Latin, is almost identical to Say's (1824) original description, including mention of a variant female specimen with reduced or absent maculation from the north shore of Lake Superior. LeConte (1860) also stated the range of the species as "New Hampshire, Canada, Mackinaw, Lake Superior...", mentioning no other areas. If Say had collected this species farther west than Lake Superior it would probably have been reflected in LeConte's statement of the known range at that time. If Say had collected his specimens very far east and south of Lake Superior, his statement of the range of the species would perhaps have been Canada, or Upper Canada, rather than "Northwest Territory". It seems probable that Say's type locality for *C. longilabris* was somewhere along the north shore of Lake Superior. Say's (1824) description of blackish color, head and thorax tinged with green, white labrum "nearly as long as broad", elytra with rather large, dense punctures, humeral and posthumeral spots, reclivate, nearly transverse middle band and subapical spot, are all characters typical of *C. longilabris* in northwestern Ontario .

A male specimen from Silver Islet, Sibley Provincial Park, Ontario, is designated as neotype and that place as type locality. The neotype specimen's label reads "Ont.: Thunder Bay Distr.: Sibley Prov. Pk. 1 km W of Silver Islet on Perry Bay." The neotype and three paraneotype specimens, one male and two females, are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Geographic variation and subspecies.— Adults of *C. longilabris* are uniform in most characters among populations across the Acadian, Great Lakes-St. Lawrence and Boreal regions and the northern part of the montane forest region in western Canada (Fig. 39). This form typically exhibits a white labrum (Fig. 12), proepisternum varying between metallic black and green, green, or green and bronze (Fig. 14), ventral abdominal color of metallic green and blue (Fig. 16), humeral lunule consisting of a humeral and/or posthumeral spot, occasionally connected (Fig. 22), a thin, elbowed middle band (Fig. 24), apical lunule consisting of one subapical spot (Fig. 26), and most specimens have between one and five per cent of the elytral surface covered by these markings (Fig. 20). This is the nominate subspecies *C. longilabris longilabris* Say.

Notable variant populations of this form are those from the island of Newfoundland, and to a lesser extent the adjacent mainland of Québec and Labrador which contain specimens with a green colored dorsum (Fig. 18). As shown in the discriminant analysis section, specimens from the island of Newfoundland are, on average, slightly larger in body size than are those from the mainland. I do not recognize these populations as taxonomically distinct from the nominate form.

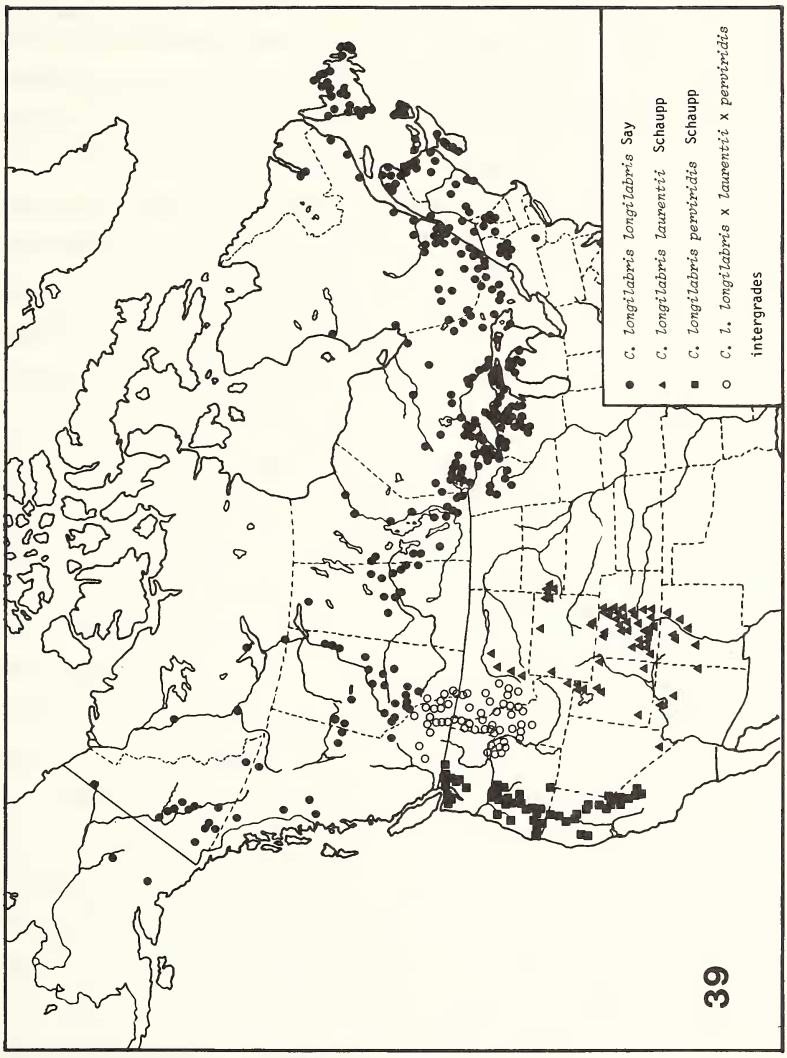


Fig. 39. Known distribution of *Cicindela longilabris* Say.

There is considerable morphometric variation among populations of the Pacific region from southern British Columbia to central California, and in the Rocky Mountain region from southwestern Alberta to Arizona and New Mexico. There is also considerable variation in qualitative characters.

In the Pacific coast states of Washington, Oregon and California most specimens have a metallic green proepisternum (Fig. 14) and abdomen (Fig. 16) and higher frequency of green dorsal coloration (Fig. 18) than specimens of the nominate subspecies. A notable exception is the OR2 population which is more variable in all three characters than other populations in the region (Figs. 14, 16, 18). The green elytral surface occurs in all specimens of the Washington state samples (Fig. 18) and becomes slightly less frequent southwards through Oregon to California.

The pattern of markings on the elytra is expanded in specimens of the Pacific region over that of typical *C. l. longilabris* (Fig. 20). This is due to an increase in the extent of all three of the lunules (Figs. 22, 24, 26). Notable exceptions are specimens of the Oregon populations, OR1 being similar to the other Pacific coast populations in the middle band (Fig. 24) and apical lunule (Fig. 26) character states, while OR2 is similar to the nominate form of the species in characters of the elytral markings.

In populations of the Rocky Mountain region of the United States there is a notable increase in bronze coloration of the proepisternum (Character states 6 and 7, Fig. 14) and an increase in the frequency of brown, bronze and olive green coloration of the dorsal elytral surface (character state 2, 3, and 4, Fig. 18). The maculations on the elytral surface are increased in Rocky Mountain populations as compared to those of the nominate form in the Boreal zone (Fig. 20, 22, 24, 26). The bronze proepisternal color, brown-bronze-olive green elytral color and development of the pattern of markings of the elytra reach their maximum frequency in CO1, CO2, UT2 and UT3 populations. These characters are variable within this region, possibly because of geographical fragmentation of the montane forest habitat of these beetles. As indicated in the discriminant analysis of morphometric data and in the pattern of variation in color (Figs. 14, 16, 18) and pattern of markings on the elytra (Figs. 20, 22, 24, 26), there are a few geographically isolated populations which vary noticeably from the form of the typical *C. l. laurentii* of central Colorado. Specimens of the Black Hills of South Dakota (SD1) exhibit somewhat reduced maculation similar to that of specimens of the boreal regions (Figs. 20, 22, 24, 26), but they exhibit variable coloration (Figs. 14, 16, 18) and occur in an isolated area of coniferous forest and dominant soil type similar to that of the Rocky Mountains of central Colorado, and parts of Wyoming and Montana. The populations from Sandoval County (NM1) and Bernalillo County (NM2), New Mexico are similarly isolated populations which consist of specimens with reduced maculation (Figs. 20, 22, 24, 26), variable coloration (Figs. 14, 16, 18) and are morphometrically different (Spanton, 1983) from those of neighbouring populations.

Samples from Iron County, Utah (UT3), Kaibab Plateau, Arizona (AZ1) and Apache County, Arizona (AZ2) represent geographically isolated populations which

are visibly differrent from each other. UT3 is distinct in exhibiting the most consistently heavily maculated specimens of any population in the species complex (Figs. 20, 22, 24, 26), AZ1 specimens exhibit a pattern of maculation which is reduced from that of surrounding populations and AZ2 specimens differ only in being slightly more variable in coloration of the proepisternum and dorsal elytral surface than those of most of the neighbouring populations. Rumpp (unpublished) has proposed subspecific names for these latter three populations. I believe that although these three populations (AZ1, AZ2, UT3) are zoogeographically interesting, the designation of a formal trinomen for each would not improve our understanding of variation in this species.

Based on the preceding discussion, the morphometric differences among the populations of the Pacific region, Rocky Mountain region and Boreal region presented in the discriminant analysis section, and zoogeographical factors, and despite the fact that the application of subspecific names to morphologically heterogeneous groupings of populations is somewhat controversial, I recognize two subspecies in addition to the nominate form *C. longilabris longilabris* discussed previously.

The subspecies *C. longilabris perviridis* Schaupp here includes the populations of the Sierra Nevada and Cascade Mountains from east-central California to southwestern British Columbia (Fig. 39), typified by an increased frequency of green elytral color, and increased elytral maculation relative to the nominal form, a smaller average body size than *C. longilabris* or *C. l. laurentii* and a proportionately longer, narrower pronotum than the nominate form.

The subspecies *C. longilabris laurentii* Schaupp, includes the populations of the Rocky Mountain region from Arizona and New Mexico to Montana, specimens of which are typified by brown to bronze or olive green dorsum (Fig. 18), bronze proepisternum (Fig. 14), and elytral maculation (in most specimens) increased over that of the nominate subspecies. The arid area of the Great Basin provides a geographic separation between *C. l. laurentii* and *C. l. perviridis* (Fig. 39).

An area of hybridization occurs where the ranges of the three subspecies converge geographically in southwestern Alberta, northwestern Montana, northern Idaho, western Washington and southeastern British Columbia (Fig. 39). The population sample AB6 from the Pincher Creek area of Alberta is an example of a hybrid population. The series of specimens was collected the same day at the same local site. Specimens in the series exhibit each of the various color states of the proepisternum (Fig. 14), all but one of the color states of the abdomen (Fig. 16), and all of the color states of the elytra (Fig. 18). The complete range of pattern is represented, from completely immaculate specimens to specimens with 20 per cent of their elytral surface covered with white markings. More intensive field collections of large series of specimens from this area are required for a detailed study of the pattern of hybridization between the forms.

Distribution.— The geographic range of *C. longilabris* is shown in Figure 39. In eastern North America the southern limit approximates the southern limit of Podzols as the dominant soil type, and the southern limit of the ranges of Jack Pine (*Pinus banksiana* Lamb.), White Spruce (*Picea glauca* (Moench) Voss), Balsam Fir (*Abies balsamea* (L.) Mill) and Balsam Poplar (*Populus balsamifera* Linnaeus) (Little, 1971). Across the prairie provinces the southern limit of the distribution of *C. longilabris* corresponds with the southern limit of boreal forest and boreal forest-grassland transition, and in the western United States the range of this species approximates the range of montane and subalpine forests, or the Canadian life zone of Merriam (1898). In the north the range of *C. longilabris* appears to be limited by the northern limit of wooded country and the southern limit of continuous permafrost.

A complete list of locality data is in the archives of the University of Alberta, and is available on request to the Department of Entomology. Included here is a list of those localities which I consider to be in the hybrid zone mentioned above. The number of specimens and the collection(s) where they are housed is indicated, or alternately, the reference is cited.

C. l. longilabris X C. l. laurentii X C. l. perviridis Intergrades

CANADA.

Alberta: Beaver Mines, 20 km W Pincher Creek (35, LU), Banff (14, CNC; 6, CU; 1, UMAA; 4, AMNH; 102, CAS), 4.5 mi N Banff (43, AMNH), Frank (1, CNC), Ft. McLeod "Brit. Amer" (1, AMNH), Loggan (20, AMNH; 1, CAS), Waterton Lakes (3, CNC). *British Columbia*: Ainsworth (1, CU), Creston (6, CNC; 4, CU; 2, UMAA; 40, UBC; 42, AMNH; 16, CAS), Fernie (5, CAS), Golden (2, AMNH), Hosmer (Leffler, 1979), Kaslo (3, CU; 7, UMAA; 19, AMNH; 2, CAS), Loiggan (1, CU), Little Vermillion River (Leffler, 1979), Sanca (2, UBC), Wynndel (12, CNC; 1, UBC; 7, AMNH; 8, CAS; 1, UAE), Yoho Valley (Leffler, 1979).

UNITED STATES.

Idaho: Benewah Co.: Emerald Creek (Leffler, 1979), N. S. Ski Bowl (1, UIM), Potlach 21.5 mi NE (Leffler, 1979). Bonner Co.: Clark Fork 8 mi E (3, UIM), Preist Lake (1, UIM), Preist River Exp. For. (1, UIM), Trout Creek 12 mi SE Sandpoint (6, UIM). Boundary Co.: Brush Lake (2, UIM), Caribou Cr. 17 mi W Naples (2, UIM), Ruby Pass 13 mi NW Naples (1, UIM). Clearwater Co.: Elk River 3 mi N (1, UIM). Elmore Co.: Atlanta (Leffler, 1979). Idaho Co.: Kooskia 15 mi E (2, REA), Lolo Pass (1, UIM), Moose Creek (15, USU), Moose Creek R. S. Grangeville (5, REA). Kootenai Co.: Coer D'Alene (3, CAS; 1, UIM). Latah Co.: Bovill (1, WSU), Flat Creek (1, REA), Harvard (1, UIM), Harvard 7 mi SE Sand Creek (1, WSU), Little Bear Cr. Helmer (1, UIM), Moscow Mtn. (7, UIM; 1, SMEK; 2, WSU), Moscow, 6 mi NE (1, UIM; 3, WSU), Troy (4, UIM). Lemhi Co.: Gibbonsville (1, UIM), Meadow Lake 6 mi N Gilmore (7, UIM). Shoshone Co.: Pine Creek (3, CMP), Wallace (2, UIM). Valley Co.: Egger's Creek (Leffler, 1979), McCall (9, UIM), Yellow Pine (1, UIM). Localities of unknown counties: Spelling (1, WSU), Lk. Waha (1, UIM; 1, CAS). *Montana*: Deer Lodge Co.: Lost Creek Pass (1, CNC). Flathead Co.: Kila, 8 mi S (Leffler, 1979). Glacier Co.: St. Mary's (1, UMAA). Jefferson Co.: Homestake Pass (Leffler, 1979). Lewis and Clark Co.: Helena (2, CAS), Roger's Pass Summit 20 km W Lincoln (1, LU). Missoula Co.: (2, USU), Blue Mountain (Leffler, 1979), Greenhough (Leffler, 1979), Kitchen Creek (Leffler, 1979), Missoula (1, MSU; 1, USNM), Pattee Canyon (Leffler, 1979). Ravalli Co.: Blodgett Mtn. (1, MSU), Blue Nose Peak (2, AMNH; 2, WSU), Camp Creek (1, MSU), Come Lake (2, AMNH), Darby (1, MSU), Darby 19 mi SW (Leffler, 1979), East Fork (1, AMNH), Girds Creek (5, MSU; 1, CAS), Hamilton (1, CNC; 2, MSU; 1, AMNH), Hamilton 6 mi NW (Leffler, 1979). Sanders Co.: Kaniksu Nat. For. Bull R. Campground (1, SMEK), Thomson Falls (2, CAS), Weeksville (MCZ), White Pine (Leffler, 1979). Silver Bow Co.: Butte (1, MSU). Localities of

unknown counties: Camp Pleasant (1, CAS), Flathead Nat. For. Big Creek (1, CMP), Glacier Park (1, CU), Glacier Park, Indian Ridge (2, AMNH), Glacier Park, McGee Meadow (1, AMNH). *Oregon*: Umatilla Co.: Athena Wild Horse Mtn. (1, AMNH), Bone Springs Blue Mtn. (12, AMNH), Meacham (2, CAS), Tollgate (11, AMNH; 2, CAS). Union Co.: Oregon Trail Camp (1, SMEK). Localities of unknown counties: Moffat Head, Blue Mtns. (1, CAS), Wallowa Mtns.: Chimney Lake (2, USU), Minam L. Area (1, WSU), Morcastle Lake (1, WSU). Additional Oregon records from Leffler (1979): Baker Co.: Anthony Lake; Baker; Pine Creek nr. Baker; Durkee. Grant Co.: Summit Dixie Pass. Umatilla Co.: Deadman's Pass. Union Co.: Elgin; Phillips Canyon 6.8 km NE Elgin; 8 mi E LaGrande. Wallowa Co.: Hat Point; French Forest Camp; Lost Line River; Wallowa Lake. *Washington*: Columbia Co.: Blue Mtns. Tollgate Road (1, WSU). Pend Oreille Co.: 7 mi W. Locke (3, PSU). Stevens Co.: Blackwelder (1, UWM). Walla Walla Co.: Walla Walla (1, WSU). Additional Washington records from Leffler (1979): Columbia Co.: Blue Mtns., Goodman Springs: Lewis Peak. Whitman Co.: Pullman.

Cicindela nebraskana Casey

Cicindela nebraskana Casey, 1909:268. Type locality: Nebraska. Casey, 1914:18. Leffler, 1979:484. Boyd and Associates, 1982:6.

Cicindela montana LeConte, 1861:338 (not Charpentier, 1825). Type area: Valleys of the Bitter Root Mountains of eastern Idaho and western Montana (here restricted: see 'Notes about synonymy and taxonomic history'). Casey, 1914:17.

Cicindela longilabris montana LeConte, 1875:157. Schaupp, 1884:87. Leng, 1902:122. Harris, 1911:20.

Cicindela longilabris nebraskana; Harris, 1911:20.

Cicindela montana canadensis Casey, 1913:17. Type locality: Calgary Alberta.

Cicindela spissitarsis Casey, 1913:18. Type locality: Aweme, Manitoba. Casey, 1914:17.

Cicindela canadensis Casey, 1914:17.

Cicindela calgaryana Casey, 1914:17. Type locality: Lethbridge, Alberta.

Cicindela montana uteana Casey, 1924:12. Type locality: Provo, Utah.

Cicindela longilabris chamberlaini; Knaus, 1925:182. Type locality: "Stein Mountains", Steens Mountains, Harney Co., Oregon.

Cicindela montana montana; Wallis, 1961:49.

Cicindela montana spissitarsis; Wallis, 1961:50.

C. montana chamberlaini; Wallis, 1961:50.

C. montana montana; Leffler and Pearson, 1976:33.

Cicindela nebraskana chamberlaini Knaus; Leffler, 1979:486. Boyd and Associates, 1982:6. **New Synonymy.**

Recognition.— Adults of *C. nebraskana* are distinguished from *C. longilabris* adults by the relatively smooth elytral surface with punctations occurring in discrete fashion, with smooth fields between, normally black abdomen varying to metallic purple or blue or blue and green in a small percentage of specimens, absence of humeral and apical lunules, and, in most specimens, absence of middle band, black dorsal coloration in the majority of specimens, and a labrum which is light tan in color in 44.8%, intermediate colored or mottled in 30.6% and black in 24.6% of females, and light in 82.6%, intermediate or mottled in 15.6%, and black in 1.8% of male specimens. Descriptions of *C. nebraskana* are found in LeConte (1861) under the name *C. montana*, and in Leng (1902), Casey (1909) and more recently, Leffler (1979).

Notes about synonymy and taxonomic history.— LeConte's (1861) name *C. montana* is a junior homonym of *C. montana* of Charpentier, (1825), itself a junior synonym of *C. hybrida riparia* Dejean (Huber, 1969). *Cicindela nebraskana* Casey 1909 is the oldest available junior synonym, and therefore becomes the correct name of the taxon.

LeConte (1861) indicated the type area for his *Cicindela montana* as "Valleys of the Rocky Mountains". Two specimens of his type series of three (housed at the Museum of Comparative Zoology, Harvard University) bear the locality data "Bitter Root" on their labels. These specimens were very probably collected in the Bitter Root Mountains of eastern Idaho and western Montana, and I have restricted the type area, accordingly.

Casey's names *C. spissitarsis*, *C. canadensis* and *C. calgaryana* are based on individual variants. Casey's (1924) name *C. montana uteana* was based on one specimen from Provo, Utah which exhibited a slightly cupreous brown dorsal coloration and more metallic luster than is typical of the species. A few specimens of *C. nebraskana* in that area exhibit some metallic green and blue abdominal color and a slightly bronze brown dorsal coloration.

Knaus's *C. l. chamberlaini* (1925) is based on a series of specimens in which a number have a slender middle band which occurs in other specimens of this species.

Geographic variation.— The frequency of occurrence of females with a dark colored labrum varies greatly between localities, but a geographic pattern is not evident (Fig. 13). The color of the proepisternum is black in most specimens of most populations sampled, (Fig. 15) but a significant number of specimens in Manitoba, Idaho, Wyoming and Utah population samples are metallic green, blue, or bronze. The color of the abdomen is also variable in some populations (Fig. 17). Populations AB2 and MT1 include many specimens with a brown abdomen and MB1, WY1, WY2, and UT1 have many specimens exhibiting metallic greens and blues.

Elytral color varies little in *C. nebraskana*. In most populations a majority of specimens have a black dorsum (Fig. 19). UT1 is a variable population with a larger number of specimens exhibiting some brown or dark olive green elytra.

Most specimens in all populations of *C. nebraskana* are immaculate or very nearly so (Figs. 21, 23, 25, 27). In those populations (ID1, WY2, Fig. 21) where the percentage of the elytral surface covered with maculations is slightly increased, it is because of the presence of a thin or incomplete middle band in some of the specimens (Fig. 25). In all of the sampled populations the humeral lunule and apical lunule (Figs. 23, 27) are absent in the majority of specimens.

Leffler (1979), in studying tiger beetles of the northwestern United States recognized two subspecies, *C. n. nebraskana* east of the continental divide, and *C. n. chamberlaini* west of the divide, based on a statistical difference in head width, the eastern form having broader heads, on average. Head width was not selected in discriminant tests 5 and 6 as a variable contributing significant variance to the discriminant functions (Table 10). In the discriminant analysis section I reported longer average femur lengths and elytral lengths in populations west of the divide, which suggests that western populations of this species are larger in body size, on average than eastern populations. These findings are not significant justification for subspecific recognition. I treat *C. nebraskana* as a monobasic species.

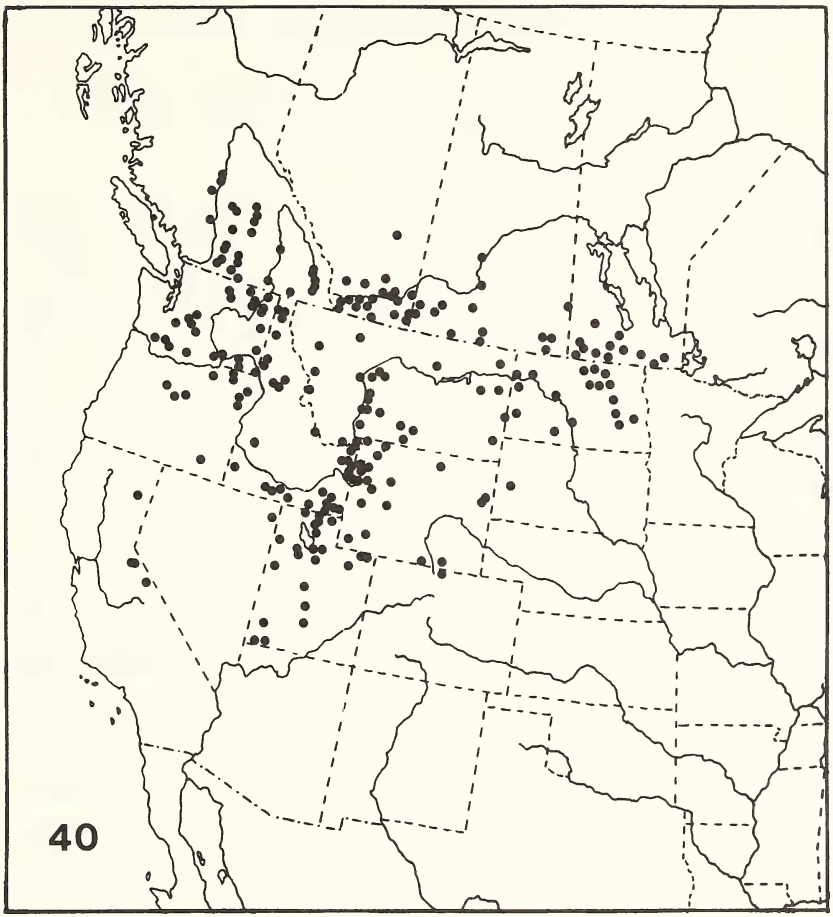


Fig. 40. Known distribution of *Cicindela nebraskana* Casey.

Distribution.— The geographic distribution of *C. nebraskana* is illustrated in Figure 40. The northern limit of the distribution of this species approximates the northern limit of Chernozemic soils in grassland and grassland-forest transition zones across the prairie provinces of Canada and in British Columbia. In the west its range follows that of the Ponderosa pine-bunchgrass vegetation zone. The range of *C. nebraskana* is limited to the south by arid lands of the Great Basin. Conditions affecting the eastern limits of the distribution of this species are unclear, but probably involve edaphic factors which are not evident at the order and great group level of soil classification.

A complete list of locality data is in the archives of the University of Alberta and is available on request to the Department of Entomology.

GENITALIA AND EVOLUTIONARY ASPECTS OF THE *CICINDELA SYLVATICA* SPECIES GROUP

Genitalia of the *C. sylvatica* group

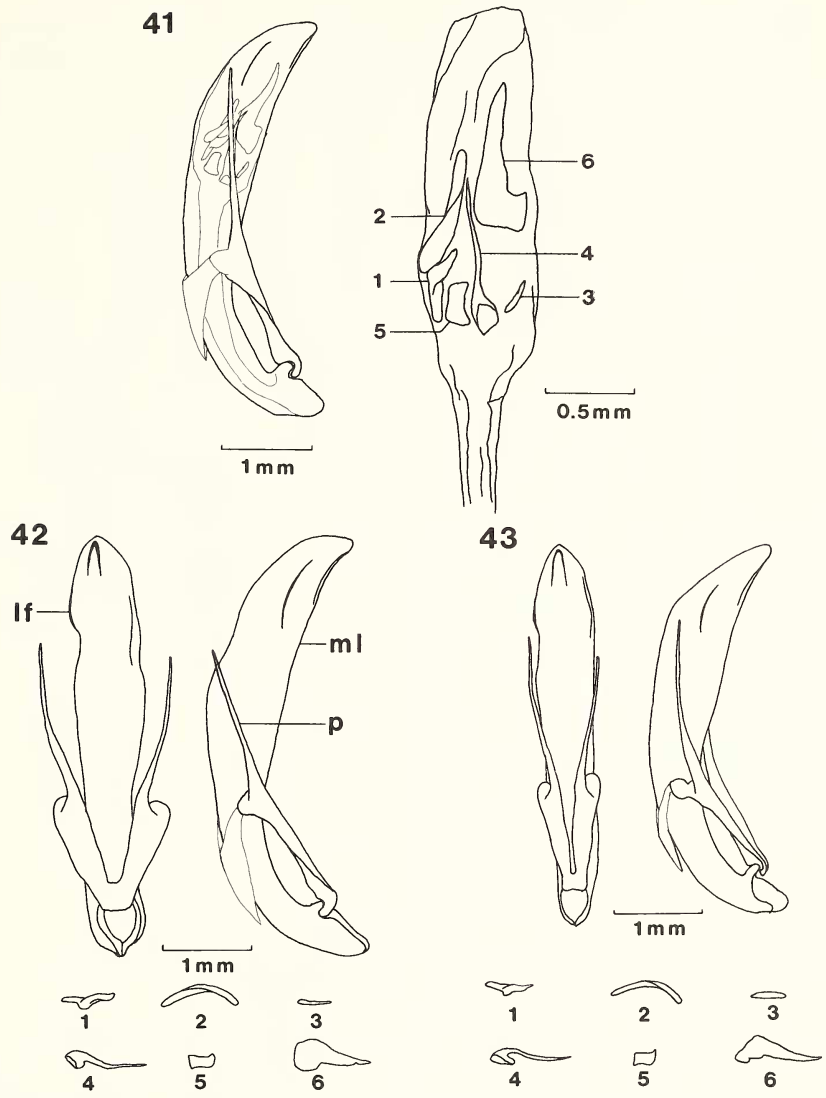
Rivalier (1950, 1954), in classifying the Palearctic and Nearctic *Cicindela* concluded that *C. longilabris* (which presumably included *C. nebraskana*) and the Palearctic species *C. soluta* Dejean, *C. lacteola* Pallas, *C. japana* Motschulsky, *C. gemmata* Faldermann, *C. sylvatica* Linneaus and *C. granulata* Gebler form a group of closely related species based on similarities of the sclerotized structures of the internal sac of the male aedeagus.

Previously the male genitalia of *C. soluta* and its geographic variation were studied by Mandl (1936), and Papp (1952) figured the male genitalia of *C. longilabris*. Mandl (1970) examined the male genitalia of *C. sylvatica* and described a new subspecies, *C. sylvatica reiseri*, based partly on slight differences in the sclerites of the internal sac.

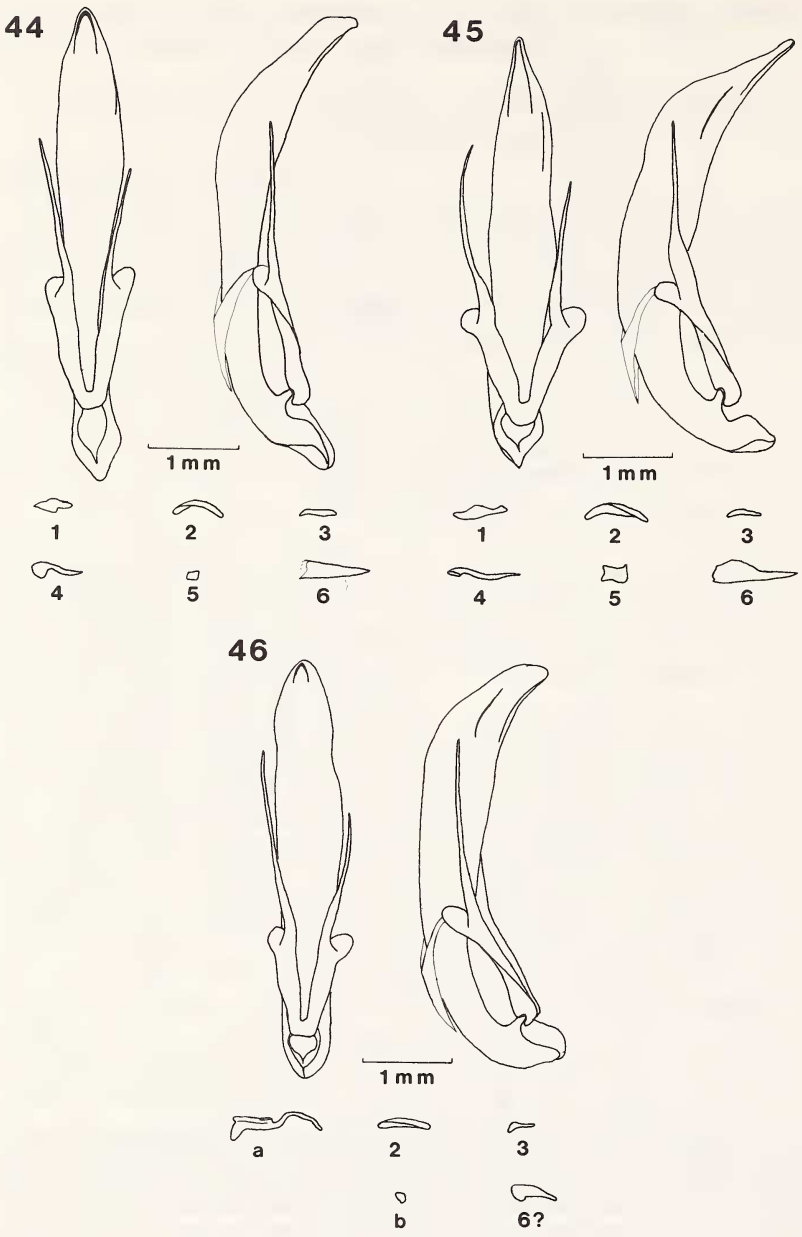
Drawings of the dorsal view, in its fully extruded state, and left lateral view of the male aedeagus and the sclerites of the internal sac are here presented for the species of the *sylvatica* group of Rivalier (1950, 1954) (Figs. 41–49). Figures 50 to 57 illustrate the female genitalia of the species of the same group. The nomenclature applied here is that of Freitag *et al.* (1985).

Figures 41 and 42 illustrate male genitalia of *C. longilabris*. The median lobe of the aedeagus is of moderate length, curved in lateral view, with lateral flanges at the apical 0.25 of its length, which converge towards the apex producing a ventrally curved point. The left lateral apical flange is usually slightly more pronounced than that on the right. The parameres (Fig. 42) are usually 0.66 to 0.75 of the length of the median lobe and taper to thin pointed apices. In all of the approximately 90 examined male specimens of the *C. sylvatica* group the right paramere is shorter than the left. In 23 measured specimens the right paramere averaged 85% of the length of the left, with a range of 78% to 99%. Figure 41 shows the arrangement of sclerites of the internal sac of the aedeagus of *C. longilabris*. The numbered sclerites are probably homologous with the correspondingly numbered structures on the internal sac in the *C. maritima* group as described by Freitag (1965). The largest is number 6, the median tooth, "la grande dent" of Rivalier (1950). The flagellum, "le flagelle" of Rivalier (sclerite 4, Figs. 41, 42), is a long, tapering sigmoid-shaped structure, thickened at its base, and pointed apically. A small sclerite 3, "le clou" of Rivalier (1950) is ventral to the base of the flagellum. The large curved sclerite 2, "la piece arciforme" of Rivalier (1950) and a smaller twisted sclerite 1, "la baguette" of Rivalier (1950) are situated dorsally in the internal sac (Fig. 41).

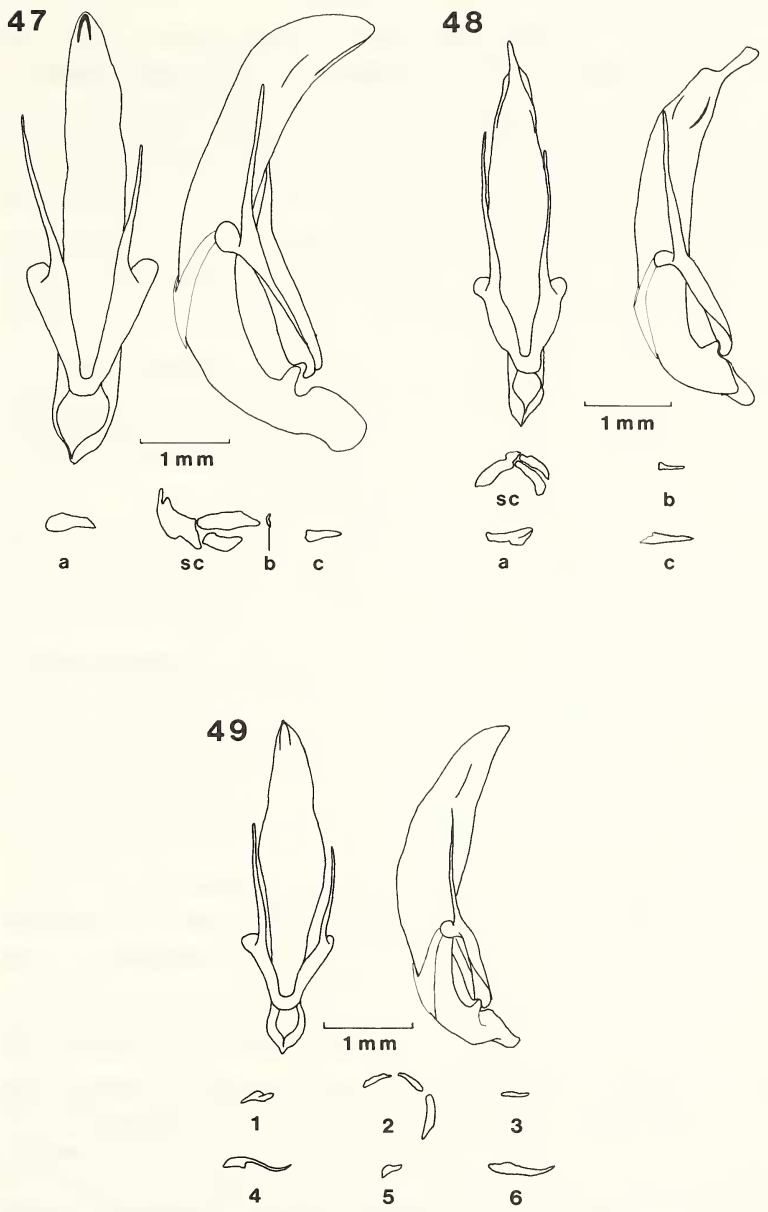
The lateral flanges (Fig. 42) are more pronounced in some individuals, but no taxonomically significant variation was found in development of lateral flanges,



Figs. 41–43. Aedeagus, left lateral aspect (extruded in mating position) and left lateral aspect of internal sac showing internal sclerites of *C. longilabris* Say from Stanley Hill Cemetery, Thunder Bay District, Ontario. (Fig. 41). Aedeagus, dorsal and left lateral aspects (extruded in mating position) and sclerites of the internal sac of *C. longilabris* Say from Gander, Nfld. (Fig. 42). Aedeagus, dorsal and left lateral aspects and sclerites of the internal sac of *C. nebraskana* Casey, from 10 mi. east of Patricia, Alberta. (Fig. 43). Legend: lf, lateral flange; ml, median lobe; p, paramere; 1, sclerite 1, probably homologous with sclerite 1 of Freitag (1965), "la baguette" of Rivalier (1950); 2, sclerite 2, probably homologous with sclerite 2 of Freitag (1965) and "la pièce arciforme" of Rivalier (1950); 3, sclerite 3, probably homologous with sclerite 3 of Freitag (1965) and "le clou" of Rivalier (1950); 4, flagellum, homologous with sclerite 4 of Freitag (1965), "le flagelle" of Rivalier (1950); 5, sclerite 5, probably homologous with sclerite 5 of Freitag (1965); 6, median tooth, "la grande dente" of Rivalier (1950), possibly homologous with sclerite 6 of Freitag (1965).



Figs. 44–46. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. sylvatica* Linnaeus from Baikal, Siberia, USSR (Fig. 44); *C. granulata* Gebler from Turkestan, USSR (Fig. 45), and *C. japana* Motschulsky from Kanazawa, Japan (Fig. 46). Sclerites of the internal sac are numbered as in Figures 28 and 29, except where homologies are uncertain: a, possibly a fusion of sclerites 4 and 5; b, sclerite of uncertain homology.



Figs. 47–49. Aedeagus, ventral and left lateral aspects, and sclerites of the internal sac of *C. gemmata* Faldermann from Korea (Fig. 47), *C. soluta* Dejean from Hungary (Fig. 48), and *C. lacteola* Pallas labelled "Turk" (Fig. 49). Legend: a, b, c, sclerites of unknown homologies; sc, sclerite cluster.

shape of aedeagus, or sclerites of the internal sac among the sampled populations of *C. longilabris*.

Male genitalia of *C. nebraskana* (Fig. 43) exhibit inter-population variation no greater than intrapopulation variation. There may be slightly more pronounced flanges of the median lobe in *C. nebraskana* than in *C. longilabris* but larger series of specimens would have to be examined to adequately test that hypothesis. Norman Rumpp (unpublished data) has found a statistical difference in the size of the genitalia between *C. nebraskana* and *C. longilabris* where the species occur sympatrically in east central California. The former has a longer aedeagus and longer median tooth of the internal sac, consistent with the larger overall body size of *C. nebraskana* relative to the smaller form of *C. longilabris* which occurs in the area (Rumpp, unpublished data).

Figure 44 shows the male genitalia of *C. sylvatica*. The median lobe of the aedeagus is different from that of *C. longilabris* or *C. nebraskana* in its long narrow apex. The flagellum (sclerite 4) of *C. sylvatica* is short and stout and the median tooth (sclerite 6) lacks the expanded base evident in the two Nearctic species. Sclerites 1, 2, and 5 (Fig. 44) are relatively small in size.

The male genitalia of *C. granulata* (Fig. 45) are distinguished by the thick median lobe with an acutely pointed apex and the stout flagellum which is not greatly thickened at its base, relative to that of *C. longilabris* (Fig. 42), *C. nebraskana* (Fig. 43) or *C. sylvatica* (Fig. 44).

The median lobe of *C. japana* (Fig. 46) is intermediate in shape between that of *C. longilabris* or *C. nebraskana* (Figs. 41, 42) and the narrower, elongated shape of *C. sylvatica* (Fig. 44). The sclerites of the internal sac distinguish *C. japana* . Sclerite a (Fig. 46) could be the result of a fusion of the flagellum (sclerite 4) and sclerite 5, but this is uncertain. Sclerites 2 and 3 (Fig. 46) are small in size and sclerite 6 is probably a reduced median tooth. The homology of sclerite b in Figure 46 is uncertain.

The male genitalia of *C. gemmata* are shown in Figure 47. The median lobe of the aedeagus is large, consistent with the large size of the beetle and is markedly curved in lateral view. The most notable character is the sclerite cluster of the internal sac (Fig. 47).

The male genitalia of *C. soluta* (Fig. 48) are smaller in size, consistent with the small body size of the beetle, and are unique among the species of the *sylvatica* group in the shape of the projection at the apex of the aedeagus. The sclerite cluster of the internal sac (Fig. 48) is similar to the sclerite cluster of *C. gemmata* (Fig. 47). Structure c in Figures 47 and 48 could possibly be the median tooth (sclerite 6) reduced in size and lacking the enlarged base present in *C. longilabris* (Figs. 41, 42). The homologies of other sclerites of the internal sac of *C. gemmata* and *C. soluta* are unclear.

The male genitalia of *C. lacteola* (Fig. 49) are distinct in the size and shape of the median lobe of the aedeagus and the semi-circular ring of sclerites in the internal

sac which probably represent an enlargement and breaking up of sclerite 2. Sclerite 6 (Fig. 49), the median tooth of the internal sac in *C. lacteola* is narrower at its base, and slightly more curved than that of other species in the species group.

Figure 50 shows the female genitalia of *C. longilabris*. Individuals vary slightly in the size and shape of the oviduct sclerite, the degree of development of the ventral notches of the second gonacoxae, and may vary markedly in the shape of the apex of the second gonapophyses. The second gonapophyses may, in some older individuals showing signs of much abrasion, wear down to 0.50 the length depicted in Figure 50. No taxonomically significant differences in female genitalic structures were observed, among populations of *C. longilabris*.

The female genitalia of *C. nebraskana* (Fig. 51) and *C. longilabris* are not clearly separable.

The female genitalia of the Palearctic species *C. sylvatica* (Fig. 52) show no characters that are distinctly different from *C. longilabris* and *C. nebraskana*, although syntergum 9 and 10 of the former species is slightly more rounded.

The female genitalia of the Palearctic species *C. granulata* (Fig. 53) are distinct in having a relatively short, wide oviduct sclerite, two small sclerotized structures visible in the right side of the bursa copulatrix and a slightly narrower syntergum 9 and 10 with lateral margins straighter than those of *C. sylvatica*.

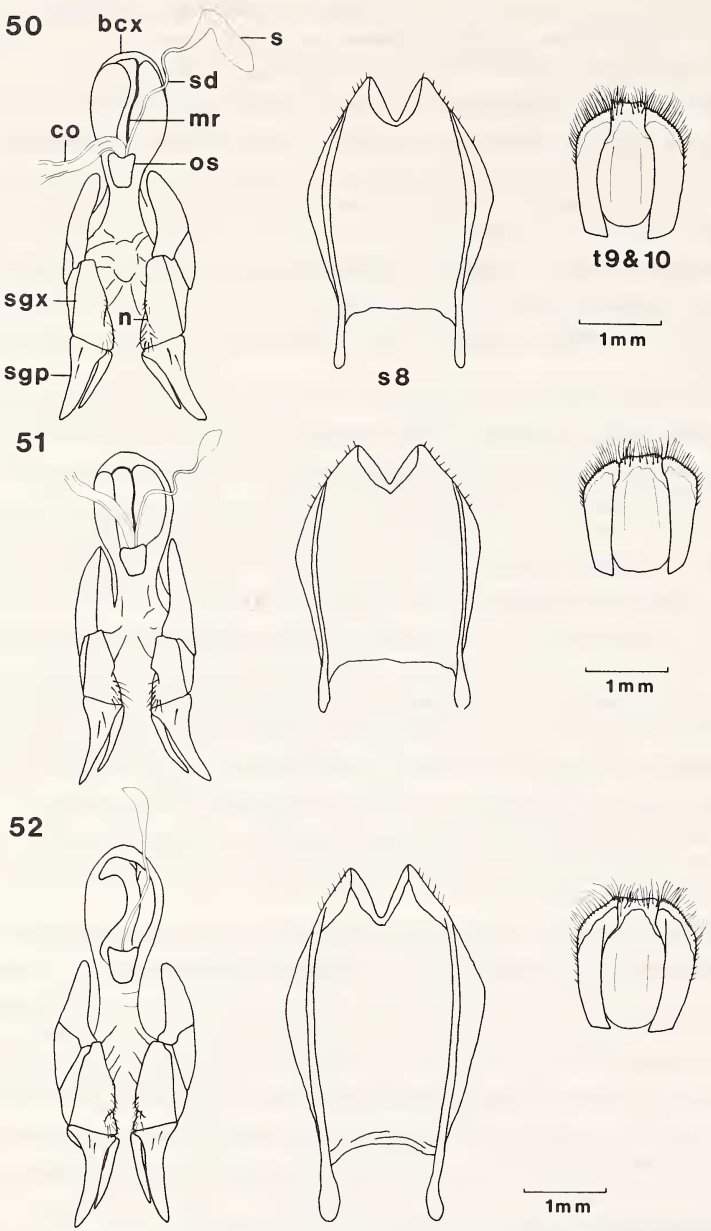
The female genitalia of *C. japana* (Fig. 54) are distinguished by the combination of a large oviduct sclerite, a small, quadrate sclerite in the membrane between the second gonacoxae, and rounded apices of sternum 8. The rounded apices of sternum 8 of this specimen (Fig. 54) may be largely a result of wear, as there are no setae on the apices and the second gonapophyses showed signs of much abrasion. The few female specimens of *C. japana* I was able to examine were all old and worn.

The female genitalia of *C. gemmata* (Fig. 55) are distinct in having a wide, rounded, slightly triangular shaped oviduct sclerite and the notched shape of the second gonapophyses.

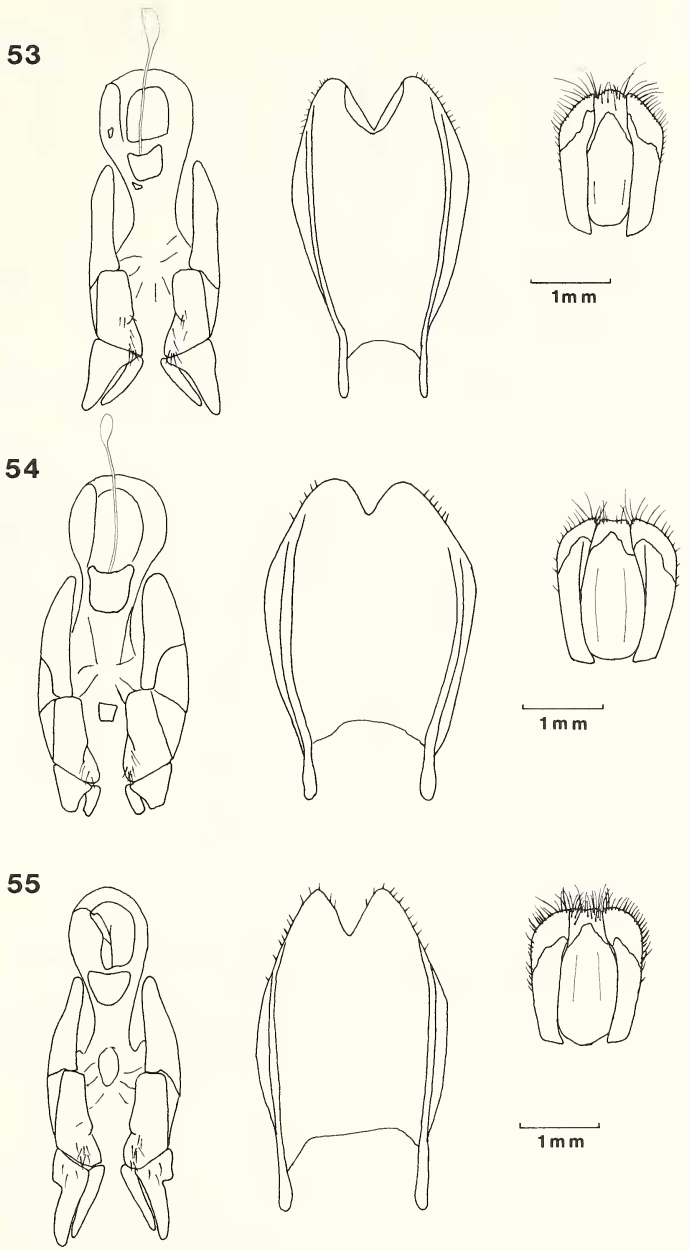
The female genitalia of *C. soluta* are distinguishable by several characters (Fig. 56). The shape of the oviduct sclerite is different from other species in the group, there is a pronounced point on the medial edge of the second gonacoxae immediately basal to the notch, the second gonapophyses have a notched shape to their lateral edge, sternum 8 is uniquely shaped at its apex with one distinct seta at a notch at the apex on each side, and the lateral portions of syntergum 9 and 10 are more rounded in shape than other species of this group. The notched lateral edge of the second gonapophyses of *C. soluta* (Fig. 56) suggests a close relationship with *C. gemmata* (Fig. 55).

The female genitalia of *C. lacteola* (Fig. 57) are distinct in the truncated setose apices of sternum 8, and the three small, dark, heavily sclerotized structures inside the bursa copulatrix.

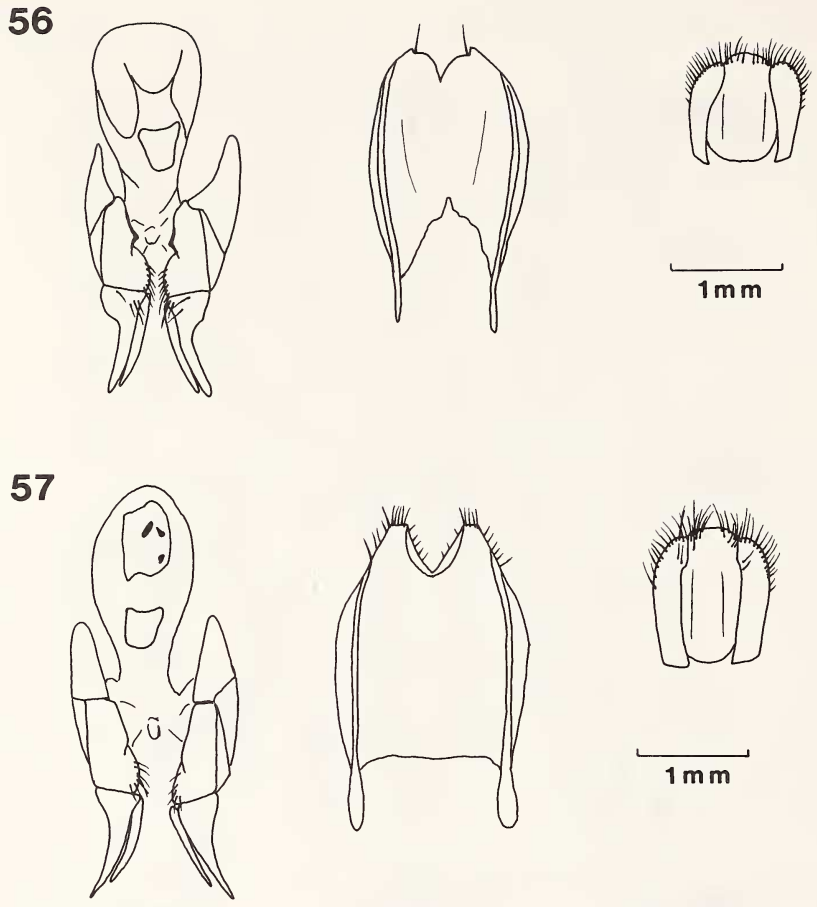
The number of setae on the ventral surface of the second gonapophyses is not useful in distinguishing species of this group, because of its variability. In *C.*



Figs. 50–52. Female genitalic structures of *C. longilabris* Say, from Harmon Field, Nfld.(Fig. 50), *C. nebraskana* Casey from 10 mi E of Patricia, Alberta (Fig. 51), and of *C. sylvatica* Linnaeus, from Baikal, Siberia, USSR (Fig. 52). Legend: bcx, bursa copulatrix; co, common oviduct; mr, median ridge of ventral sclerite of bursa copulatrix; n, ventral notch of second gonacoxa; os, oviduct sclerite; s, spermatheca; sd, spermathecal duct; sgp, second gonapophysis; sgx, second gonacoxa; s8, sternum eight, ventral aspect; t9&10, syntergum nine and ten, dorsal aspect.



Figs. 53–55. Female genitalic structures of *C. granulata* Gebler, from Turkestan, USSR (Fig. 53); *C. japana* Motschulsky from Kanazawa, Japan (Fig. 54); and *C. gemmata* Faldermann, from Kanazawa, Japan (Fig. 55). Structures are labelled in Figure 50.



Figs. 56 and 57. Female genitalic structures of *C. soluta* Dejean from Hungary (Fig. 56) and of *C. lacteola* Pallas from Aulic Ata (Fig. 57). Structures are labelled in Figure 50.

58

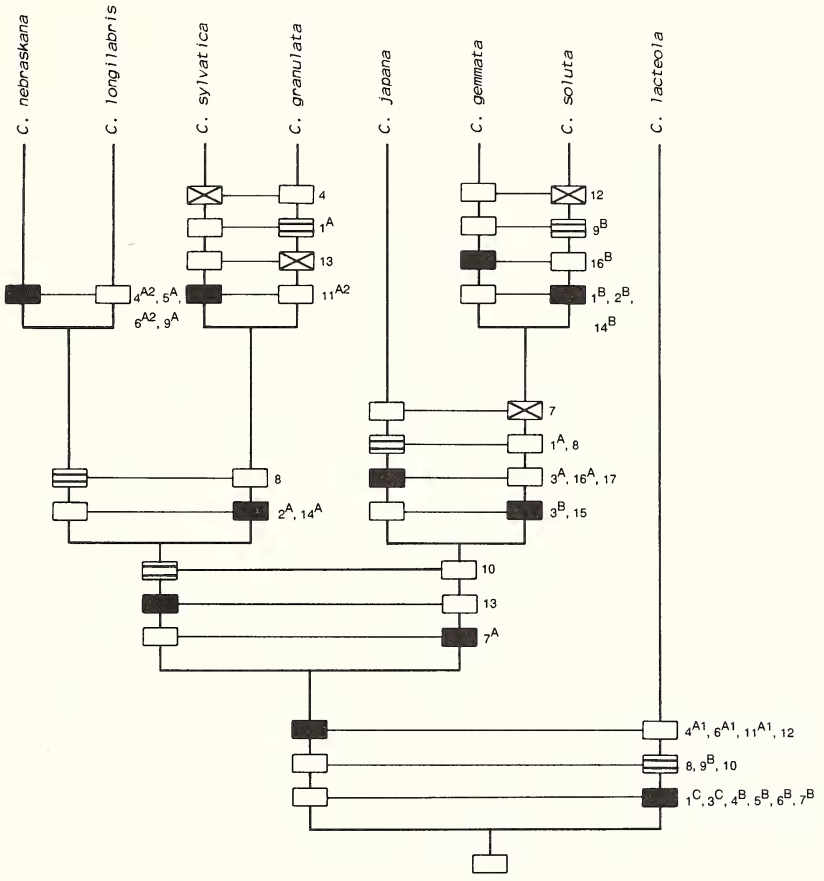


Fig. 58. Reconstructed phylogeny of the *Cicindela sylvatica* species group. Dark boxes indicate apotypies, light boxes indicate plesiotypies, crosses indicate reversals, and parallel lines indicate homoplasies. Characters (primary numbers) and character states (superscripts) are as indicated in Table 13.

longilabris this varies from zero in some individuals to four in others and differs between the right and left sides of many individuals.

Reconstructed Phylogeny

W. Horn (1926) made one of the earliest attempts to arrange some of the species of the genus *Cicindela* into species groups, based on external structure. Rivalier (1950, 1954, 1957, 1961, 1963) carried out studies of the male genitalic structures of species of *Cicindela*, and based thereon arranged the species in genera, subgenera and species groups. As Freitag (1974) indicated, Rivalier's classification has been largely accepted in North America, although Rivalier's genera have been treated as subgenera, and his subgenera as synonyms, as reflected in a recent checklist of the North American tiger beetles (Boyd and Associates, 1982).

Rivalier (1950, 1954) grouped the North American species *C. longilabris* with the Palearctic species *C. soluta* Dejean, *C. lacteola* Pallas, *C. japana* Motschulsky, *C. gemmata* Faldermann, *C. sylvatica* Linneaus, and *C. granulata* Gebler. He associated this *sylvatica* group with the *C. hybrida*, *C. transbaicalica* and *C. maritima* groups (groups I, II, and IV, respectively, of Rivalier, 1950, 1954), in what is now considered the subgenus *Cicindela*. Freitag (1974) considered the *maritima* group, among the North American fauna, to be the most closely related to *C. longilabris* and *C. nebraskana*. Both authors (Freitag, 1974; Rivalier, 1950, 1954) considered these species groups to be among the most primitive in the genus *Cicindela* . For these reasons, and because published information (Freitag, 1965, 1974), and specimens are more available to me than for either of the Palearctic *C. hybrida* and *C. transbaicalica* groups, I have used the *C. maritima* group as the outgroup for the *C. sylvatica* group, for purposes of character polarization for a phylogenetic analysis.

The methods used in phylogenetic reconstruction have been discussed by Hennig (1966), Ross (1974), Wiley (1981), and Watrous and Wheeler (1981), among many others. Basically, such an analysis involves the identification of the sister group of the taxon to be analysed, shared character states are assumed to have been inherited from a common ancestor (in this study an ancestor common to both the *sylvatica* and *maritima* species groups), and are designated as plesiotypic (primitive or ancestral). Apotypic (derived) character states are then used as evidence of phylogenetic affinity, or relative recency of common ancestry, between the species, or taxa sharing such character states.

Phylogenetic analysis of character states.— Characters are listed numerically, in the sequence in which they appear in Table 13 and Figure 58, and plesiotypic and apotypic states are specified for each. The notation used by Ball (1985) is here used, in which apotypic states believed to be part of multi-state transformation series are numbered consecutively, the lowest numbered state being most like the plesiotypic state. Apotypic states believed to have evolved independently from the plesiotypic condition are indicated by different capital letters.

01. *Female genitalia, 8th sternum.* Four states: plesiotypic, with angular, pointed apices (Figs. 50–52); apotypic state A, with rounded apices (Figs. 53, 54); apotypic state B, each apex with a notch bearing a stout seta (Fig. 56); apotypic state C, apices truncate, with 5 or 6 setae at apical margin (Fig. 57).

02. *Male genitalia, apex of aedeagus.* Three states: plesiotypic, apex of aedeagus narrowed to a rounded point (Figs. 41–43); apotypic state A, apex of aedeagus prolonged (Figs. 44, 45); apotypic state B, apex of aedeagus with a laterally flattened projection (Fig. 48).

03. *Male genitalia, sclerites of the internal sac.* Four states: plesiotypic, six distinct sclerites present (Figs. 41–45); apotypic state A, sclerites 4 and 5 fused (Fig. 46a); apotypic state B, sclerite cluster 'a' present (Figs. 47, 48); apotypic state C, sclerite 2 divided into three parts (Fig. 49).

04. *Humeral lunule configuration* (Fig. 6). Four states: plesiotypic, complete lunule (Fig. 8(4)); apotypic state A1, lunule reduced to two dots (Fig. 8(3)); apotypic state A2, absent from most specimens; apotypic state B, lunule expanded and continuous with markings.

05. *Middle band configuration* (Fig. 6). Three states: plesiotypic, lunule present; apotypic state A, lunule absent; apotypic state B, lunule broadened and continuous with other markings.

06. *Apical lunule configuration* (Fig. 6). Four states: plesiotypic, lunule complete; apotypic state A1, reduced to one spot; apotypic state A2, lunule absent completely; apotypic state B, lunule expanded and continuous with other markings.

07. *Elytra, color of dorsal surface.* Three character states: plesiotypic, grey-brown to black; apotypic state A, brown and metallic green and/or blue; apotypic state B, metallic red to bronze.

08. *Frons, presence or absence of setae* (other than supro-orbital setae).Two states: plesiotypic, present; apotypic, absent.

09. *Elytra, surface texture.* Three character states: plesiotypic, roughly granulate, appearing dull to the unaided eye; apotypic state A, finely granulate with slight depressions surrounded by smooth fields, appearing shiny to the unaided eye; apotypic state B, finely granulate, appearing smooth to the unaided eye.

10. *Labrum, shape, length/width.* Two states: plesiotypic, short; apotypic, long.

11. *Labrum, shape of median longitudinal ridge.* Three states: plesiotypic, absent (labrum flat, or nearly so); apotypic state A1, broad, rounded median ridge; apotypic state A2, median ridge in the form of a sharp carina.

12. *Body size.* Two character states: plesiotypic, medium sized *Cicindela*; apotypic, large sized *Cicindela.*

13. *Labrum, color.* Two states: plesiotypic, light tan color; apotypic, dark brown to black color, at least in some individuals.

14. *Antennal scape, "other setae"* (Fig. 3). Three states: plesiotypic, zero to four in number; apotypic state A, four to 10 in number; apotypic state B, more than 20. The 20+ number of setae found at this locus on the scape in specimens of *C. soluta* was interpreted as having been independently derived from the plesiotypic state because *C. soluta* shares two good synapotypies with *C. gemmata,* and because this character is sufficiently labile among species of *Cicindela* that I could not assume that the condition was derived from the four to 10 state exhibited by *C. sylvatica* and *C. granulata* (Table 13, Fig. 58).

15. *Female genitalia, second gonapophyses.* Two states: plesiotypic, with smoothly curved lateral margins (Figs. 50–54); apotypic, with notched lateral margins (Figs. 55, 56).

16. *Female genitalia, oviduct sclerite.* Three states: plesiotypic, shield shaped (Figs. 50–53); apotypic state A, larger in size (Fig. 54); apotypic state B, triangular shaped (Fig. 55).

17. *Female genitalia, quadrate sclerite in membrane between 2nd gonacoxae.* Two states: plesiotypic, quadrate sclerite absent; apotypic, quadrate sclerite present (Fig. 54).

For characters which vary within a taxon, that state exhibited by the majority of specimens over most of the geographic range of the species was coded for cladistic analysis. For example, character 7, color of the elytral surface, is quite variable in *C. longilabris* including bronze to dull green specimens for *C. l. laurentii* in the Rocky Mountain region, and some green specimens of *C. l. longilabris* in Newfoundland, and *C. l. perviridis* in California and Oregon, to predominantly black or dark brown over most of the range of the species. *Cicindela longilabris* was coded as "0" because the plesiotypic dark brown or black color exhibited by specimens in most of the geographic range of the species. A similar coding strategy was applied for *C. longilabris* for the characters of the elytral markings (characters 4,5,6), all of which show some variation in this taxon.

Reconstructed Phylogeny.— The reconstructed phylogeny appears in Figure 58. The first branching point on the cladogram is a divergence of *C. lacteola* from the common ancestor of the other seven species in the group. *Cicindela lacteola* exhibits a number of autapomorphies, including distinctly truncate, setose apices of sternum eight (character 1), sclerite two of the internal sac divided into three parts (character 3), humeral lunule, middle band and apical lunule expanded and confluent (characters 4, 5, 6), and a metallic red -bronze elytral color (character 7). The remaining seven species in the group share an apotypically reduced humeral lunule (character 4), an apical lunule reduced to a single spot (character 6), labrum with a broad rounded median ridge (character 11), and a larger body size (character 12). *Cicindela japana, C. gemmata* and *C. soluta* share the apotypic color of the elytra (character 7). *Cicindela gemmata* and *C. soluta* share an apotypic sclerite cluster 'a' of the internal sac of the male aedeagus (character 3), and the notched second gonapophyses of the female genitalia (character 15). The ancestor of *C. nebraskana, C. longilabris, C. sylvatica,* and *C. granulata* is assumed to have had an apotypically dark colored labrum (character 13), a condition which is assumed to have reversed to its plesiotypic state in *C. granulata. Cicindela sylvatica* and *C. granulata* share a prolonged apex of the aedeagus (character 2), and an increased number of 'other setae' on the antennal scape (character 14). *Cicindela nebraskana* and *C. longilabris* both exhibit setae on the frons (character 8), which are lacking in *C. sylvatica* and *C. granulata.*

Homoplasies were invoked to explain the distribution of characters 1, 8, 9, 10, and 14, and reversals were required in characters 4, 6, and 12. I placed emphasis on (informally weighted) characters of the male and female genitalia (characters 1, 2, 3, 15, 16, 17), the labrum (characters 10, 11, 13), and presence of setae on the frons (character 8), and less emphasis on characters such as elytral maculations (characters 4, 5, 6) and elytral color (character 7). I have shown that these latter characters are highly variable across the range of *C. longilabris* and the recent work of Schultz (1986) with *C. formosa*, and Acorn (in prep.) with *C. scutellaris*, show that in other tiger beetle species as well, characters of color and color pattern are extremely labile and subject to local selection. An obvious weakness of this reconstruction is that elytral color is the only synapotypy uniting *C. japana, C. gemmata* and *C. soluta.*

The lack of a synapomorphy at the basal node suggests that this group is polyphyletic: perhaps *C. lacteola*, which exhibits a number of autapomorphies, should not be classified in this species group. This lack of a basal synapomorphy for the group is based, in part, on my assumption that the apotypic long labrum (character 10) arose independently in *C. lacteola*, and in the lineage which gave rise to the species *C. nebraskana, C. longilabris, C. sylvatica,* and *C. granulata.* The alternate hypothesis, that a long labrum arose once in a common ancestor of the group, and subsequently underwent reversal to the short plesiotypic state in the clade which includes *C. japana, C. gemmata* and *C. soluta* would support the

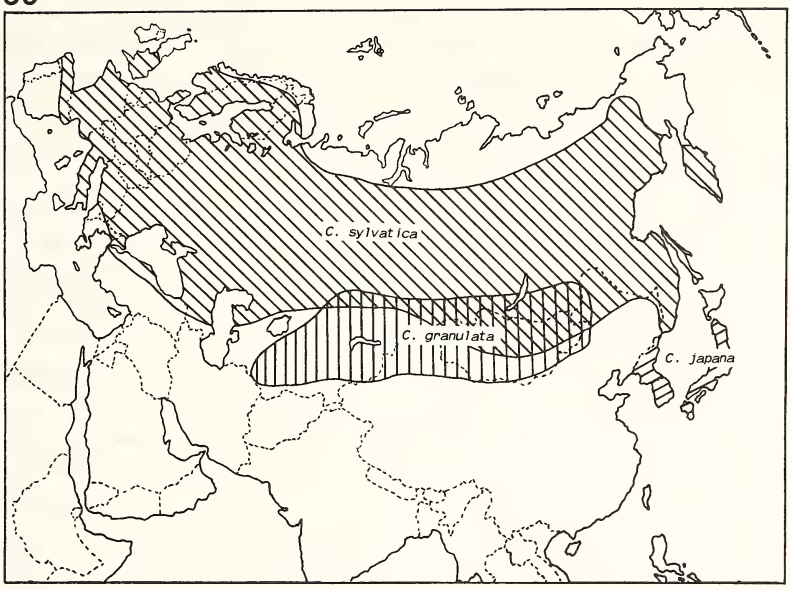
monophyly of the species group.

Evolution of characters.— Some trends in the evolution of characters in this group are worth noting. Three characters of the labrum were considered here (characters 10, 11, 13). Species in the *maritima* group exhibit relatively short, and flat labra. In the *sylvatica* group this tends toward a much longer labrum (apotypically) in proportion to its width, especially in the clade which includes *C. nebraskana*, *C. longilabris*, *C. sylvatica* and *C. granulata* It is interesting that the species with the longest labra also exhibit more pronounced median ridges, especially in *C. sylvatica*, in which the ridge is intensified into a sharp keel. The longitudinal ridge in these species may function largely to strengthen a longer labrum. It is also in this clade that a trend toward a dark colored labrum occurs. This is most pronounced in *C. sylvatica* and *C. nebraskana*, although, as discussed previously, some individuals of *C. longilabris* also possess a dark colored labrum. The adaptive significance of a longer, dark colored labrum is unknown. As mentioned above, *C. lacteola* also possesses a somewhat elongate labrum, which in this reconstruction (Fig. 58) is assumed to have arisen independently. This is assumed because the labrum of *C. lacteola* is not as elongate, nor is it associated with a trend toward increase of a median ridge and dark color, as it is in the clade which includes *C. nebraskana, C. longilabris, C. sylvatica* and *C. granulata.*

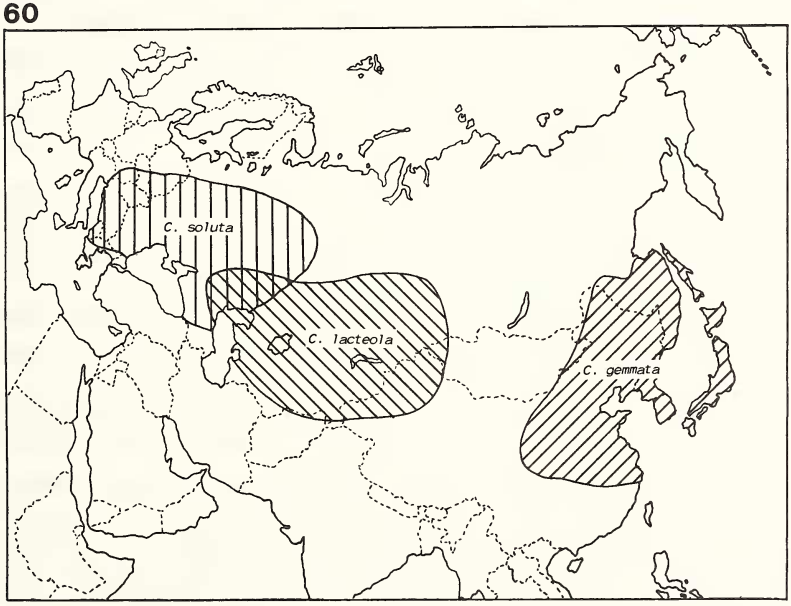
The most apotypic characters of the genitalia are found in species which are plesiotypic with respect to labral characters. Most notable are the sister species *C. gemmata* and *C. soluta* which, as mentioned above, share the apotypically notched second gonapophyses (character 15) and the sclerite cluster (character 3, B) of the internal sac of the male aedeagus. Pronounced autapotypies occur in the shape of the apex of the eighth sternum (character 1) in females of *C. soluta* and *C. lacteola*, the triangular-shaped oviduct sclerite (character 16) of females of *C. gemmata* and *C. japana*, and in the shape of the apex of the aedeagus (character 2) in males of *C. lacteola.* The functional significance of such genitalic characters has yet to be suggested.

Independent and opposite states have evolved in the pattern of markings on the elytral surface (characters 4, 5, 6) from the ancestral state in which each of the markings is present and complete. In *C. lacteola* the markings have become broadened and confluent. In several species of the group there is a trend toward reduction in markings, with the humeral and apical lunules incomplete, present as one or two dots. This is carried to an extreme in *C. nebraskana* in which the elytral markings are absent, in most specimens. The pattern of markings on the elytral surface is very labile. As noted previously, such characters are highly variable within the species *C. longilabris* and may be subject to reversals and homoplasy among species, thus great emphasis should not be placed upon such characters in reconstructing a phylogeny.

59



60



Figs. 59–60. Approximate geographic distributions of the Palearctic species of the *Cicindela sylvatica* group. 59. *C. sylvatica* Linnaeus, *C. granulata* Gebler, and *C. japana* Motschulsky. 60. *C. soluta* Dejean, *C. lacteola* Pallas, and *C. gemmata* Faldermann.

Geographical History

Introduction.— I offer a few remarks concerning the possible history of differentiation of the species *C. nebraskana* and *C. longilabris* and their immediate relatives, according to the hypothesized phylogeny (Figure 58), *C. sylvatica* and *C. granulata*. A detailed account of the evolutionary history of all members of the group is not possible at present, as there is a paucity of information concerning the distribution and habitat affinities of the Palearctic species.

The pattern.— The geographic ranges of *C. nebraskana* and *C. longilabris* are presented in Figures 38 and 40, respectively. As mentioned previously, *C. longilabris* is primarily a species of boreal forest and mixed coniferous/deciduous forests, from Newfoundland to Alaska, north as far as tree line and south to the southern limit of spruce (*Picea* spp.) and Jack Pine (*Pinus banksiana*) in the east, and is also found in montane and subalpine forests in the mountains of western North America as far south as Arizona and California. *Cicindela nebraskana* is primarily a species of grasslands and forest/grassland transition zones in the western prairies and in the Pacific Northwest. The approximate ranges of *C. sylvatica* and *C. granulata* are presented in Figure 59. *Cicindela sylvatica* occurs from western Europe (United Kingdom, France, and Scandinavia) east across coniferous forest and mixed forest regions of the northern part of the Palearctic region to eastern Siberia. *Cicindela granulata* occurs in a narrow band stretching in an east to west direction, approximately coincident with the grassland regions of central Asia. The approximate distribution of *C. japana* is also shown in Figure 59. Figure 60 shows the approximate distributions of *C. lacteola*, *C. gemmata*, and *C. soluta*. Little is known of the habitat affinities of these Palearctic species. Their collective ranges are restricted to temperate regions.

Age of the C. sylvatica group.— The age of the *C. sylvatica* group is, in the absence of a fossil record, largely speculative. Willis (1967) stated that the cicindelids arose during the Permian, and that the genera of tiger beetles arose during the Mesozoic. Freitag (1965) thought that the ancestral stock of the *C. maritima* group was in existence in the early Tertiary. The warmest Cenozoic climatic period for the northern hemisphere was during the mid Eocene, at which time paratropical forests were thought to occur as far north as present day arctic regions (Matthews, 1979a). Subsequent to the Eocene maximum, a gradual cooling and increase in latitudinal climatic gradient are thought to have occurred, culminating in the onset of glacial conditions in the northern Hemisphere during the late Pliocene. As most species of the *C. sylvatica* group occur in the Palearctic Region, it seems likely that this predominantly northern lineage had its beginnings in the expanding temperate forests of the Palearctic region sometime subsequent to the Eocene climatic maximum, perhaps during the Oligocene.

Differentiation of the species.— If we assume, as suggested above, an origin of the group in Oligocene temperate forests of the Palearctic, then a common ancestor of *C. nebraskana*, *C. longilabris*, *C. sylvatica* and *C. granulata* must have been in

existence in the late Oligocene or Miocene. Geological evidence suggests that an Asian-Alaskan land connection has existed from the late Cretaceous to the Pliocene, and it is thought that a boreal realm taxonomically more diverse than today's Boreal forest was Holarctic in extent in the Miocene (Matthews, 1979a). Such an ancestral species could have had a Holarctic or Palearctic distribution in the Miocene, and the divergence of the Nearctic lineage (*C. nebraskana* and *C. longilabris*) and the Palearctic lineage (*C. sylvatica* and *C. granulata*) could have been a result of either a vicariant or dispersal event, probably also during the Miocene, but could have occurred anytime prior to the the marine transgression of Beringia approximately 3 Mya.

The *C. nebraskana*/*C. longilabris* and *C. granulata*/*C. sylvatica* species pairs may represent parallel situations in which *C. granulata* in the Palearctic and *C. nebraskana* in the Nearctic independently invaded grassland habitats, from a coniferous forest inhabiting ancestor. This could have happened, in both instances during late Miocene or early Pliocene, as it is thought that steppe habitats were in existence in the interior of North America by the late Miocene (Matthews, 1979a, Webb, 1977).

An alternate scenario would involve a single invasion of grasslands in either the Palearctic or Nearctic Region, by a lineage which dispersed across Beringia during the Quaternary, during glacial periods when steppe floral and faunal elements from both Palearctic and Nearctic regions were present in Beringia (Matthews, 1982). This would have to have been followed by vicariant speciation during an interglacial period of the Quaternary when there was a marine barrier between Alaska and Siberia. This latter scenario is less probable than the former, for two reasons. It would imply that *C. nebraskana* is most closely related to *C. granulata* which is inconsistent with the relationships indicated by structural characters of the species (Figure 58), and also requires a speciation event during a Quaternary interglacial. This seems unlikely in light of studies of fossil beetles which show that almost no speciation has occurred through the course of the Quaternary period (Ashworth, 1979; Coope, 1977, 1979; Matthews, 1979a and b, 1980; Morgan and Morgan, 1980), and that only in Miocene and Pliocene deposits does one find fossils of beetles which are specifically distinct from extant forms (Matthews, 1976, 1979b, 1980, 1982).

Similarly, it is unlikely that the ancestor of *C. sylvatica*, C. granulata, C. longilabris, and *C. nebraskana* was a savannah/grassland inhabitant, as the Beringian connection between Asia and the New World in the Late Tertiary was predominantly a coniferous forest biome. Savannah and grasslands were found farther south, in the interior of Asia and North America. As mentioned above, there was an exchange of steppe biota via the Beringian steppe-tundra habitats of the Pleistocene, but a steppe inhabiting ancestor would have had to expand across Beringia in the Pleistocene, followed by a subsequent speciation event separating the ancestor of *C. longilabris*/*C. nebraskana* from the ancestor of *C. sylvatica*/*C.*

granulata. Then two more, independent speciation events would have had to occur to produce the four species we see today, presumably also in the Pleistocene. This much speciation during the Pleistocene seems unlikely in light of fossil beetle evidence which shows a remarkable constancy of form and lack of speciation in the last two or more million years (Coope, 1979; Matthews, 1976, 1979a and b, 1980, among others).

Differentiation within the Nearctic lineage.— *Cicindela nebraskana* probably diverged from a common ancestor with *C. longilabris* sometime during the Miocene, associated with the increase of grassland habitats in the interior of North America. Subsequently, *C. nebraskana* has remained monobasic, showing relatively little variation, compared with *C. longilabris* which is a polymorphic species. This could be a result of *C. nebraskana* having passed the Quaternary glacial periods in semi-arid regions of western North America, south of the ice fronts, in a contiguous, if somewhat restricted geographic range possibly in the northern part of the Great Basin region. *Cicindela longilabris*, in contrast, may have developed intraspecific variation, and subsequent differentiation of subspecies as a result of fragmentation of its range during glacial periods of the late Pliocene and Pleistocene. It is possible that over the past two to three million years, during glacial periods, the range of *C. longilabris* was compressed southward, and fragmented, with what is now the nominate form *C. l. longilabris* having been isolated in spruce forests, which are thought to have occurred in a belt across the eastern two-thirds of the continent, south of the ice fronts (Watts, 1983; Ruhe, 1983). At the same time, populations ancestral to *C. l. laurentii* might have been isolated in montane forests in the Rocky Mountain region, and populations ancestral to *C. l. perviridis* were isolated in the Sierra Nevada/Cascade Mountains in the Pacific region. Climatic conditions during the relatively long glacial periods may have thus reduced genetic mixing among what we now see as subspecific entities, while acting to maintain the genetic continuity within the subspecies. For example, in the southern Rocky Mountains of Arizona and New Mexico, Spaulding *et al.* (1983) have shown that some subalpine tree species occurred during glacial episodes at elevations more than 1000 meters below their present lower altitudinal limit. This would mean that some populations of *C. l. laurentii* which are today isolated in forested areas of the Colorado Plateau, the Wasatch and Uintah Mountains of Utah, the Abajo Mountains of southeastern Utah, and the White Mountains of eastern Arizona may have had some genetic contact during the periods of coldest climate via increased areas of coniferous forest habitat. Thus the present pattern of geographic variation among and within the subspecies of *C. longilabris* may have developed during Pleistocene climatic cycles involving long glacial periods during which the subspecies of *C. longilabris* were isolated, and populations within subspecies were genetically mixed, alternating with relatively short interglacial periods during which the three subspecies mixed in a hybrid zone, as seen today (Figure 39). Some temporary isolation of populations occurred within subspecies (especially in the southern Rocky Mountain populations

of *C. l. laurentii* as seen today), and the range of the nominate subspecies *C. l. longilabris* expanded northward with coniferous forest habitats.

CONCLUDING REMARKS

Questions requiring additional research have been presented in places throughout the text. At the risk of some repetition I suggest the following.

Additional insight into the relationships between populations of *C. longilabris*, especially in the western part of North America, relative to the interspecific differences between *C. longilabris* and *C. nebraskana* might be gained by electrophoretic studies. Additional field studies in the grassland-forest transition regions of the western prairies, and in the Pacific Northwest might better elucidate the nature of the ecological separation between the two species in question, and I believe edaphic factors should figure prominently in such investigations. More information concerning distribution, patterns of geographic variation, and habitat affinities of the Palearctic species of the *C. sylvatica* group would aid greatly in determining phylogenetic relationships in the group. Laboratory mating of adults and rearing of larvae of the Palearctic species would add larval characters to the information available for cladistic analysis of the group. Perhaps more importantly, a rigorous phylogenetic analysis of the genus *Cicindela* is needed to test the monophyly of the present supraspecific groupings. After such a cladistic framework is established, phylogenetic analysis at the species group level will be on a much more secure basis than at present.

ACKNOWLEDGEMENTS

I thank R. Freitag, sponsor of my M.Sc. program, for his advice and encouragement during the course of this study, and the members of my advisory committee, A. D. Macdonald, R. J. Ross, and J. P. Ryder, for their help and advice. I thank my external examiner, G. E. Ball, and my colleagues J. H. Acorn and B. V. Brown for constructive criticisms of the text.

I greatly appreciate the help and patience of the curators and private collectors listed under "Materials", who kindly loaned specimens. I thank A. Newton, T. L. Erwin, and G. W. Byers for the courtesies extended during visits to their respective establishments. Thanks are also extended to M. Palmer and to C. B. Knisely for their courtesy and hospitality during visits, and for helpful discussions of rearing techniques and field methods. I extend my thanks to W. Johnson and to D. Brzoska, for kindly inviting me into their homes to examine collections of tiger beetles, and to N. L. Rumpp, for sharing with me his unpublished metric data for male genitalia of several populations of *C. longilabris* and *C. nebraskana*. I also appreciate the many useful discussions of tiger beetle biology, evolution and taxonomy with M. M. Kaulbars.

Special thanks are due to Y. Spanton for technical assistance, and for much patience throughout.

Financial support is gratefully acknowledged from the following sources: during most of the duration of this study, from National Sciences and Engineering Research Council Grant A4888 held by R. Freitag, and during the final stages of preparation of this manuscript, from NSERC Grant A1399 held by G. E. Ball.

LITERATURE CITED

Ashworth, A. C. 1979. Quaternary Coleoptera studies in North America: past and present. pp. 395–406. *In* T. L. Erwin, G. E. Ball, and D. R. Whitehead (Eds.) Carabid Beetles: Their Evolution, Natural History, and Classification. Proceedings of the First International Symposium of Carabidology. Dr. W. Junk, bv Publishers, The Hague. 635 pp.

Ball, G. E. 1985. Reconstructed phylogeny and geographical history of genera of the tribe Galeritini (Coleoptera: Carabidae). pp 276–321. *In* G. E. Ball (Ed.): Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. Dr. W. Junk Publishers, Dordrecht. xiii + 514 pp.

Barrowclough, G. H. 1982. Geographic variation, predictiveness, and subspecies. The Auk 99:601–602.

Boyd, H. P. and Associates. 1982. Checklist of Cicindelidae: The Tiger Beetles. Plexus Publishing, Inc., Marlton, New Jersey. 31 pp.

Casey, T. L. 1909. Studies in the Caraboidea and Lamellicornia. The Canadian Entomologist 41:253–268.

Casey, T. L. 1913. Studies in the Cicindelidae and Carabidae of America. Memoirs on the Coleoptera 4:1–92. New Era Publishing Company, Lancaster, P.A.

Casey, T. L. 1914. Studies in *Omus* and *Cicindela*. Memoirs on the Coleoptera 5:1–24. New Era Publishing Company, Lancaster, P.A.

Casey, T. L. 1924. Additions to the known Coleoptera of North America. Memoirs on the Coleoptera 11:1–347. New Era Publishing Company, Lancaster, P.A.

Charpentier, Toussaint de. 1825. Horae Entomologicae, Adjectis Tabulis Novem Coloratis, Apud A. Gosohorsky, Bibliopolam, Wratislaviae. 255 pp.

Clayton, J. S., W. A. Ehrlich, D. B. Cann, J. H. Day, and I. B. Marshall. 1977. Soils of Canada. Research Branch, Canada Department of Agriculture. Printing and Publishing, Supply and Services Canada. Ottawa, Canada. 3 vols.

Coope, G. R. 1977. Quaternary Coleoptera as aids in the interpretation of environmental history. pp. 55–68. *In* F. W. Shotton (Ed.) British Quaternary Studies: recent advances. Clarendon Press, Oxford. 298 pp.

Coope, G. R. 1979. Late Cenozoic Fossil Coleoptera: Evolution, Biogeography, and Ecology. Annual Review of Ecology and Systematics 10:247–267.

Criddle, N. 1907. Habits of some Manitoba "Tiger Beetles" (*Cicindela*). The Canadian Entomologist 39:105–114.

Criddle, N. 1910. Habits of some Manitoba Tiger Beetles (Cicindelidae) No. 2. The Canadian Entomologist 42:9–15.

Dahl, R. G. 1941. The Leng types of Cicindelidae (Coleoptera). Entomological News 52:169 and 188–189.

Dejean, P. F. M. A. 1825, 1826, 1828, 1829, 1831. Species général des Coléoptères de la collection de M. LeCompte Dejean, Paris. 1:I-XXX, 1–463; 2:I-VIII, 1–501; 3:I-VII, 1–566; 4:I-VII, 1–250; 5:I-VII, 1–883.

Dejean, P. F. M. A. 1837. Catalogue des Coléoptères de la Collection De M. LeCompte Dejean. Paris. 3ème ed. 176 pp.

Dunn, G. A. 1978. Tiger Beetles of New Hampshire (Coleoptera: Cicindelidae). M.S. Thesis, University of New Hampshire, September, 1978.

Edwards, J. G. 1954. A new approach to intraspecific categories. Systematic Zoology 3:1–10.

Emmons, E. 1854. The natural history of New York Agriculture. IV. Coleoptera. Gould, Kendall and Lincoln, Albany. 272 pp.

Freitag, R. 1965. A Revision of the North American species of the *Cicindela maritima* group with a study of hybridization between *Cicindela duodecimguttata* and *oregona*. Quaestiones Entomologicae 1:87–170.

Freitag, R. 1974. Selection for a non-genitalic mating structure in female tiger beetles of the genus *Cicindela* (Coleoptera: Cicindelidae). The Canadian Entomologist 106:561–568.

Freitag, R., L. A. Schincariol, and B. L. Barnes. 1985. A review of nomenclature for genitalic structures of *Cicindela*. Cicindela 17:117–127.

Gaumer, G. C. 1977. The variation and taxonomy of *Cicindela formosa* Say (Coleoptera: Cicindelidae). Ph.D. Dissertation, Texas A & M University, 253 pp.

Gill, F. B. 1982. Might there be a resurrection of the subspecies? The Auk 99:598–599.

Gosline, W. A. 1954. Further thoughts on subspecies and trinomials. Systematic Zoology 3:92–94.

Goulet, H. and B. R. Baum. 1981. Analysis of variation in the *Elaphrus americanus* complex of North America (Coleoptera: Carabidae). Canadian Journal of Zoology 59:2253–2274.

Goulet, H. and B. R. Baum. 1982. Analysis of variation in the *Elaphrus finitimus* complex of North America (Coleoptera: Carabidae). Canadian Journal of Zoology 60:2424–2433.

Graves, R. C. 1963. The Cicindelidae of Michigan (Coleoptera). American Midland Naturalist 69:492–502.

Graves, R. C. 1965. The distribution of tiger beetles in Ontario. (Coleoptera: Cicindelidae). Proceedings of the Entomological Society of Ontario 95:63–70.

Hamilton, C. C. 1925. Studies on the Morphology, Taxonomy, and Ecology of the larvae of Holarctic tiger beetles (Cicindelidae). Proceedings of the United States National Museum 65:1–87.

Harris, E. D. 1911. List of North American Cicindelidae in the Harris Collection. Truan Press, Yonkers, NY. 68 pp.

Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana, Illinois. 263 pp.

Heppner, J. B. and G. Lamas. 1982. Acronyms for World Museum Collections of Insects, with emphasis on Neotropical Lepidoptera. Bulletin of the Entomological Society of America 28:305–316.

Hori, M. 1982. The biology and population dynamics of the tiger beetle *Cicindela japonica* (Thunberg). Physiology and Ecology Japan 19:77–212.

Horn, W. 1915. Genera Insectorum: Coleoptera, Adephaga, family Carabidae, subfamily Cicindelinae. Louis Desmet-Verteneuil, Brussels. Fasc. 82C (1915).

Horn, W. 1926. Carabidae: Cicindelinae. Coleopterorum Catalogus. Pars 86:1–345. W. Junk, Berlin.

Horn, W. 1928. Notes and records in the tiger beetles of Minnesota. Minnesota Agricultural Experiment Station Technical Bulletin 56:9–13.

Horn, W. 1930. Notes on the races of *Omus californicus* and a list of the Cicindelidae of America North of Mexico (Coleoptera). Transactions of the American Entomological Society 56:78–86.

Hubbell, T. H. 1954. The naming of geographically variant populations. Systematic Zoology 3:113–121.

Huber, R. L. 1969. Homonymy in the Nearctic *Cicindela*. Cicindela 1:19–22.

Huie, L. H. 1915. The bionomics of the tiger beetle *Cicindela campestris*. Proceedings of the Royal Physical Society of Edinburgh 20:1–11.

Johnson, N. K. 1982. Retain subspecies- at least for the time being. The Auk 99:605–606.

Kaulbars, M. M. 1982. Systematics and ecology of the *sexguttata* species group, genus *Cicindela* (Coleoptera: Cicindelidae). M.Sc. Thesis, Lakehead University, Thunder Bay, Ontario.

Kelly, K. L. and D. B. Judd. 1965. The ISCC-NBS Method of Designating Colors and a Dictionary of Color names. National Bureau of Standards Circular 553, and Supplement to NBS Circular 553: ISCC-NBS Color-name Charts Illustrated with Centroid Colors. United States Government Printing Office. 158 pp and 18 color charts.

Kim, J. and F. J. Kohout. 1975. Analysis of variance and covariance: Subprograms Anova and Oneway. pp. 398–433. *In* N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent, (Eds.) SPSS: Statistical Package for the Social Sciences, 2nd Ed., McGraw-Hill Inc., U.S.A.

Kirby, W. 1837. The Insects. *In* J. Richardson. Fauna Boreali-Americana 4: 12pp.

Klecka, W. R. 1975. Discriminant Analysis. pp. 434–467 *In* N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, (Eds.) SPSS: Statistical Package for the Social Sciences, 2nd Ed. McGraw-Hill, Inc., U.S.A.

Knaus, W. 1925. Three new forms of Coleoptera. Pan-Pacific Entomologist

1:182–183.

Lanyon, W. E. 1982. The subspecies concept: Then, now, and always. The Auk 99:603–604.

LeConte, J. L. 1848. A Descriptive Catalogue of the Geodephagus Coleoptera inhabiting the United States east of the Rocky Mountains. Annals of the Lyceum of Natural History of New York 5:173–186.

LeConte, J. L. 1859. The complete writings of Thomas Say on the entomology of North America 1: XXIV + 412 pp; 2: IV + 814 pp.

LeConte, J. L. 1860. Revision of the Cicindelidae of the United States. Transactions of the American Philosophical Society 11:27–63.

LeConte, J. L. 1861. New species of Coleoptera inhabiting the Pacific district of the United States. Proceedings of the National Academy of Sciences, Philadelphia 13:338–389.

LeConte, J. L. 1875. Notes on Cicindelidae of the United States. Transactions of the American Entomological Society 4:157–162.

Leffler, S. R. 1979. Tiger Beetles of the Pacific Northwest (Coleoptera: Cicindelidae). Ph.D. Dissertation, University of Washington, College of Forest Resources. 790 pp.

Leffler, S. R. and D. L. Pearson. 1976. Tiger Beetles of Washington. Cicindela 8:21–60.

Leng, C. W. 1902. Revision of the Cicindelidae of Boreal America. Transactions of the American Entomological Society 28:93–186.

Leng, C. W. 1918. A new race of *Cicindela* with notes on other races and species. Journal of the New York Entomological Society 26:138–141.

Lindroth, C. H. 1953. Kirby's types of North American Carabidae (Coleoptera). Proceedings of the Royal Entomological Society of London, Series B 22: 169 pp.

Lindroth, C. H. 1955. The carabid beetles of Newfoundland including the French islands of St. Pierre and Miquelon. Opuscula Entomologica. Supplementum 12, 189 pp.

Lindroth, C. H. 1963. The fauna history of Newfoundland illustrated by Carabid beetles. Opuscula Entomologica, Supplementum 23: 112 pp.

Lindroth, C. H. and R. Freitag. 1969. North American Ground beetles (Coleoptera, Carabidae, excluding Cicindelidae) described by Thomas Say: Designation of Lectotypes and Neotypes. Psyche 76:326–361.

Little, E. L. 1971. Atlas of United States Trees, Volume 1: Conifers and important hardwoods. United States Department of Agriculture Forest Service Miscellaneous Publication No. 1146, United States Government Printing Office, Washington, D.C.

Mandl, K. 1936. *Cicindela soluta* Dej. und ihre Rassen. Koleopterologische Rundschau 22:117–119.

Mandl, K. 1970. Kleinere Beitrage zur Kenntris der Familie Cicindelidae. Koleopterologische Rundschau 48:67.

Matthews, J. V., Jr. 1976. Insect fossils from the Beaufort Formation: Geological and Biological significance. Geological Survey of Canada. Paper 76–1B:217–227.

Matthews, J. V., Jr. 1979a. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. pp. 31–86 *In* H. V. Danks (Ed.) Canada and its insect fauna. Memoirs of the Entomological Society of Canada 108. 573 pp.

Matthews, J. V., Jr. 1979b. Late Tertiary Carabid Fossils from Alaska and the Canadian Archipelago. pp. 425–445 *In* T. L. Erwin, G. E. Ball , D. R. Whitehead and A. L. Halpern, (Eds.) Carabid Beetles: Their Evolution, Natural History, and Classification. Proceedings of the First International Symposium of Carabidology. Dr. W. Junk, bv, Publishers, The Hague.

Matthews, J. V., Jr. 1980. Tertiary land bridges and their climate: Backdrop for development of the present Canadian insect fauna. The Canadian Entomologist 112:1089–1103.

Matthews, J. V., Jr. 1982. East Beringia during the late Wisconsinan time: A review of the biotic evidence. pp. 127–150 *In* D. M. Hopkins, J. V. Matthews, Jr., C. E. Schweger, and S. B. Young, (Eds.) Paleoecology of Beringia. Academic Press, xiv + 489 pp.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill Book Company, New York. x + 428 pp.

Mayr, E. 1982. Of what use are subspecies? The Auk 99:593–595.

Merriam, C. H. 1898. Life zones and crop zones of the United States. United States Department of Agriculture, Division of Biological Surveys, Bulletin 10:9–79.

Monroe, B. L., Jr. 1982. A modern concept of the subspecies. The Auk 99:608–609.

Morgan, A. V. and A. Morgan. 1980. Faunal assemblages and distributional shifts of Coleoptera during the late Pleistocene in Canada and the northern United States. The Canadian Entomologist 112:1105–1128.

Murray, R. R. 1980. Systematics of *Cicindela rufiventris* Dejean, *Cicindela sedecimpunctata* Klug and *Cicindela flohri* Bates (Coleoptera:Cicindelidae). Ph.D. Thesis. Texas A & M University, College Station, Texas. 301 pp.

O'Neill, J. P. 1982. The subspecies concept in the 1980's. The Auk 99:609–612.

Owen, D. F. 1963. Variation in North American Screech Owls and the subspecies concept. Systematic Zoology 12:8–14.

Palmer, M. K. 1976. Natural history and behaviour of *Pseudoxychila tarsalis* Bates. Cicindela 8:61–92.

Palmer, M. K. 1978. Growth rates and survivorship of tiger beetle larvae. Cicindela 10:49–66.

Palmer, M. K. 1979. Rearing tiger beetles in the laboratory. Cicindela 11:1–11.

Palmer, M. K. and M. A. Gorrick. 1979. Influence of food on development in tiger beetle larvae. Cicindela 11:17–23.

Papp, H. 1952. Morphologische und phylogenetische untersuchungen an

Cicindela-Arten. Unter besonderer Berucksichtigung der Ableitung der nearktishen Formen. Oesterreichische Zoologische Zeitschrift 3:494–533.

Parkes, K. C. 1955. Sympatry, allopatry and the subspecies in birds. Systematic Zoology 4:35–40.

Parkes, K. C. 1982. Subspecific taxonomy: unfashionable does not mean irrelevant. The Auk 99:596–598.

Phillips, A. R. 1982. Subspecies and species: fundamentals, needs and obstacles. The Auk 99:612–615.

Rivalier, E. 1950. Démembrement du Genre *Cicindela* Linné. (Travail préliminaire limité à la faune paléartique) Revue Français d'Entomologie 17:217–244.

Rivalier, E. 1954. Démembrement du Genre *Cicindela* Linné. II. Faune Américaine. Revue Français d'Entomologie 21:249–268.

Rivalier, E. 1957. Démembrement du Genre *Cicindela* L. III. Faune Africano-Malgache. Revue Français d'Entomologie 24:312–342.

Rivalier, E. 1961. Démembrement du Genre *Cicindela* L. IV. Faune Indomalaise. Revue Français d'Entomologie 28:121–149.

Rivalier, E. 1963. Démembrement du Genre *Cicindela* L. V. Faune Australienne. Review Français d'Entomologie 30:30–48.

Ross, H. H. 1974. Biological Systematics. Addison-Wesley Publishing Co., Inc., Reading, Massachusetts; Menlo Park, California; London; Don Mills, Ontario. 345 pp.

Rowe, J. S. 1972. Forest Regions of Canada. Department of Fisheries and the Environment, Canada. Canadian Forestry Service Publication No. 13001972. Reprinted 1977. 171 pp.

Ruhe, R. V. 1983. Depositional Environment of Late Wisconsin Loess in the Midcontinental United States. pp. 130–137 *In* W. J. Wright and S. C. Porter (Eds.) Late Quaternary Environments of the United States. University of Minnesota Press.

Say, T. 1824. Coleoptera. *In* W. H. Keating. Narrative of an expedition to the source of the St. Peter's River, Lake Winipeek, Lake of the Woods, etc., etc., performed in the year 1823 by order of the Hon. J. C. Calhoun, Secretary of War, under Command of Stephen H. Long, Major U.S.T.E., H. C. Carey and I. Lea, Philadelphia. Vol. II, pp. 268–378.

Schaupp, F. G. 1884. Synoptic tables of Coleoptera: Cicindelidae. Bulletin of the Brooklyn Entomological Society 6:72–109.

Schultz, T. D. 1986. Role of Structural Colors in Predator Avoidance by Tiger Beetles of the genus *Cicindela* (Coleoptera: Cicindelidae). Bulletin of the Entomological Society of America 32:142–146.

Shelford, V. E. 1907. Preliminary note on the distribution of the tiger beetles (*Cicindela*) and its relation to plant succession. Biological Bulletin 14:9–14.

Shelford, V. E. 1908. Life histories and larval habits of the tiger beetles (Cicindelidae). Journal of the Linnaean Society of London 30:157–184.

Shelford, V. E. 1917. Color and color pattern mechanism of tiger beetles. Illinois Biological Monographs 3:395–532.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York. 247 pp.

Smith, H. M. and F. N. White. 1965. A case for the trinomen. Systematic Zoology 5:183–190.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical Taxonomy. The principles and practice of numerical classification. W. H. Freeman and Company, San Francisco. xv + 573 pp.

Soil Conservation Service. 1967. Distribution of typical kinds of soil: orders, suborders and great groups; National Cooperative Soil Survey Classification; Albers equal area projection; 1:7,500,000; 70.5 x 42 cm; colored *In* National Atlas of the United States of America, 1970. Geological Survey, United States Department of the Interior. Washington, D.C. 85–88.

Soils of Canada. 1972. Pedology and Cartographic sections of the Soil Research Institute, Research Branch, Canada Department of Agriculture, Ottawa. 1:5,000,000; Lambert conformal conic projection, standard parallels 49 degrees north and 77 degrees north, modified polyconic projection north of latitude 80 degrees.

Soil Survey Staff. 1960. Soil Classification: A comprehensive system, 7th approximation. United States Department of Agriculture, Washington, D.C. 265 pp.

Soil Survey Staff. 1967. Supplement to soil classification system. United States Department of Agriculture, Washington, D.C. 207 pp.

Southwood, T. R. E. 1978. Ecological Methods with particular reference to the study of insect populations. 2nd Edition. Chapman and Hall, London, UK. xxiv + 524 pp.

Spanton, T. G. 1983. A Revision of the Nearctic Species of the *Cicindela sylvatica* group (Coleoptera: Cicindelidae). M.Sc. Thesis, Lakehead University, Thunder Bay, Ontario. 175 pp.

Spaulding, W. G., E. B. Leopold and T. R. VanDevender 1983. Late Wisconsin Paleoecology of the American Southwest. pp. 259–293 *In* W. J. Wright and S. C. Porter (Eds.) Late Quaternary Environments of the United States. University of Minnesota Press.

Storer, R. W. 1982. Subspecies and the study of geographic variation. The Auk 99:599–601.

Tanner, V. M. 1929. The Coleoptera of Utah - Cicindelidae. Pan-Pacific Entomologist 6:78–87.

Wallis, J. B. 1961. The Cicindelidae of Canada. University of Toronto Press. 74 pp.

Watrous, L. E. and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Systematic Zoology 30:1–11.

Watts, W. A. 1983. Vegetational History of the Eastern United States 25,000 to

10,000 Years Ago. pp. 294–310 *In* W. J. Wright and S. C. Porter (Eds.) Late Quaternary Environments of the United States. University of Minnesota Press.

Webb, S. D. 1977. A history of savanna vertebrates in the New World. Part I: North America. Annual Review of Ecology and Systematics 8:355–380.

Wiley, E. O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley and Sons, New York. xv + 439 pp.

Willis, H. L. 1967. Bionomics and Zoogeography of tiger beetles of saline habitats in the central United States (Coleoptera: Cicindelidae). The University of Kansas Science Bulletin 47:145–313.

Willis, H. L. 1968. Artificial key to the species of *Cicindela* of North America north of Mexico (Coleoptera: Cicindelidae) Journal of the Kansas Entomological Society 41:303–317.

Willis, H. L. 1974. Behavioural studies of *Cicindela*. Cicindela 6:1–8.

Wilson, E. O. and W. L. Brown, Jr. 1953. The subspecies concept. Systematic Zoology 2:97–111.

Zusi, R. L. 1982. Infraspecific geographic variation and the subspecies concept. The Auk 99:606–608.